SOME EFFECTS OF TEMPERATURE AND MOISTURE UPON *MELANO-PLUS MEXICANUS MEXICANUS* SAUSSURE AND *CAMNULA PELLUCIDA* SCUDDER (ORTHOPTERA)

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OF THE UNIVERSITY OF MINNESOTA

BY

JOHN ROBERT PARKER

L C.

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

1929

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SOME EFFECTS OF TEMPERATURE AND MOISTURE UPON MELANOPLUS MEXICANUS MEXICANUS SAUSSURE AND CAMNULA PELLUCIDA SCUDDER (ORTHOPTERA)

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SOME EFFECTS OF TEMPERATURE AND MOISTURE UPON MELANOPLUS MEXICANUS MEXICANUS SAUSSURE AND CAMNULA PELLUCIDA SCUDDER (ORTHOPTERA)[1]

INTRODUCTION

Melanoplus mexicanus mexicanus Saussure[2] and *Camnula pellucida* Scudder are the two most destructive grasshoppers in the northern half of the United States and the southern part of Canada. A study of their life history and methods of controlling them was begun as an Adams Fund project at the Montana Experiment Station in 1918. As the work progressed it became more and more apparent that their development, daily activities, and seasonal abundance were to a large extent controlled by temperature and to a lesser extent by moisture. A search through the literature published prior to 1921 revealed only a few scattered references to the effects of temperature and moisture upon *M. mexicanus* and none to their effects upon *C. pellucida*. It was therefore decided to make an intensive study of the effects of these two ecological factors upon both species.

In October, 1922, the author was granted leave of absence from the Montana Experiment Station and from then until March, 1924, the work on which this paper is based was carried on at the University of Minnesota, both as a project in the Minnesota Experiment Station and as a thesis problem in the graduate school. After March, 1924, the work was continued as an Adams Fund project at the Montana Experiment Station and as a graduate thesis problem at the Montana State College.

ACKNOWLEDGMENTS

The advice and assistance of a number of persons have aided very materially in the carrying on of the experimental work and the preparation of the manuscript, and it is a pleasure to here acknowledge their generous help and hearty cooperation.

[1]This paper was submitted to the faculty of the Graduate School of the University of Minnesota in partial fulfillment of the requirements for the degree of Doctor of Philosophy, June, 1929.

[2]This grasshopper, known for years as *Melanoplus atlanis* Riley, has very recently been given the above name (6).[3] Many of the graphs were prepared before the change was made and on these the old name—*M. atlanis*—has been retained.

[3]Reference is made by number to "Literature Cited," p. 131.

Professor R. A. Cooley, under whose immediate supervision that part of the work done in Montana has been carried on, made many valuable suggestions and was a constant source of advice and counsel. To Doctor W. A. Riley, who made it possible for part of the work to be done in Minnesota, I am especially grateful. The work carried on in Minnesota was under the direct supervision of Doctor R. N. Chapman, whose insight into the more complex phases of the problem was of the greatest aid in the interpretation and treatment of the mass of data which accumulated from the field and laboratory experiments.

Professor A. G. Ruggles spent nearly a month with me gathering data under field conditions in Minnesota and in characteristic manner refused to take any credit for his part in the work. His friendly interest has been a source of much encouragement.

Doctor W. C. Cook has been consulted frequently and his assistance in the preparation of the graphs was of special value.

Helpful suggestions were received from Mr. Stewart Lockwood and Mr. R. L. Shotwell, who also generously allowed me to use some of their unpublished notes and several times furnished me with grasshopper eggs.

Messrs. E. R. Buckel, Paul Vroom, and H. L. Seamans made it possible to secure data in British Columbia during a severe outbreak of *C. pellucida* and went to considerable effort to secure material for my work. These members of the Canadian Entomological Branch gave me all possible assistance and the few days spent with them in the field were particularly enjoyable.

Finally I wish to acknowledge the aid of the following student assistants—Frank Cowan, Heber Donohoe, David Fox, Clement Griffith, Glenn Kohls, Mauro Rodriquez, and Walter Stanley. These men did a large amount of the experimental work, and whatever value this paper may have is due in no small degree to their faithfulness.

Mr. G. Allen Mail, as graduate assistant, displayed unusual ability in conducting the rearing work during one year of the project, and also prepared many of the graphs.

METHODS OF PROCEDURE

Field observations under natural conditions were made whenever possible but the greater part of the work was carried on in the laboratory under controlled temperature and humidity conditions. Both *C. pellucida* and *M. mexicanus* were studied when available, but the latter species, being more common, was used the most.

REARING METHODS

Grasshoppers were for the most part reared in cylindrical glass tubes 8 inches long and 1½ inches in diameter; in some of the work a tube 3 inches in diameter was used. The ends of the tubes were closed in various ways but the method finally chosen as the best was to cover one end with cheese-cloth held in place by a rubber band and the other with a cork in which was drilled a 1-inch hole. A piece of brass screening was cut slightly greater in circumference than the cork and fastened to it by means of small brads. When the cork is pushed into the end of the glass tube the edges of the screen are bent back and act as a spring, holding the cork tightly in place and preventing young grasshoppers from getting into the space between the tapering end of the cork and the side of the tube.

Tubes thus stoppered can be worked much faster than when cheese-cloth and rubber bands are used on both ends, and they are better ventilated than tubes with a screened cork at each end. If the end closed with cheese-cloth is slightly raised, very little moisture will condense on the inside of the tubes, even when large amounts of green stuff are placed in them for food. When large drops of water are allowed to remain in the tube, young grasshoppers crawl through them and frequently adhere to the glass with fatal results.

Sprouted wheat, wheat seedlings, corn seedlings, wandering jew *(Tradescantia),* and dried alfalfa leaves were used as food. No water was available to the caged grasshoppers other than the small amount of condensation water on the sides of the glass tubes.

Adult grasshoppers from which eggs were desired, were caged in lamp globes placed over flower pots firmly packed with clean, damp sand, which was sifted daily to recover any egg pods that might have been laid.

Several different methods of incubating and storing eggs were tried but the one finally adopted was to place them on the surface of sterilized sand in round tin boxes, 1 inch deep and 2½ inches in diameter. The sand was kept slightly damp by adding distilled water whenever needed. Boxes containing eggs were either placed in the incubating chambers or held in cold storage until ready for use.

METHODS OF CONTROLLING TEMPERATURES

In most of the rearing work the glass tubes and tin boxes containing grasshoppers and grasshopper eggs were held in specially constructed cabinets in which the temperature could be kept practically constant. Heat was furnished by ordinary Mazda lights under thermostatic control. It was found that more uniform conditions could be obtained when the temperature within the cabinet was raised to within 5° C. of the desired temperature by lights on a permanent circuit, and the exact temperature obtained by one 40-watt light under thermostatic control. When all the lamps are connected with the thermostat, fluctuations in temperature may occur, due to the fusing of the thermostat points. Seventy-five-watt Mazda lights placed 18 inches above the glass top of the cabinets furnished a constant source of light.

For temperatures ranging from 22° to 37° C. the cabinets were placed in a basement where the room temperature could be maintained between 17° and 22° C. throughout the year. For lower temperatures cabinets were built into a cold storage room where the temperature averaged from 0° to 5° C.

At the Minnesota Experiment Station somewhat similar cabinets were used and, in addition, a Carrier Air Conditioning Cabinet was available, in which any desired temperature could be obtained very quickly by the manipulation of electrical heating units and an ammonia refrigerating plant. This was of great value for making short-time observations but was not practical for comparative rearing experiments extending over considerable periods of time.

Constant low temperatures for long periods were secured in a heavily insulated cabinet in which the temperature was reduced by refrigeration coils controlled by an expansion valve.

Temperatures as low as –40° C. could be maintained in this cabinet for days at a time with a variation of less than one degree.

Low temperatures were also secured by the expansion of carbon dioxide in a coil inserted into a Dewar flask, the temperature at any particular moment being ascertained by the electrothermal method used by Carter (4).

METHODS OF CONTROLLING HUMIDITY

Obtaining constant humidity conditions was a much more difficult problem than controlling temperature. Several methods were tried, none of which proved entirely satisfactory.

A modification of Headlee's (5) method of obtaining constant relative humidities by drawing air through saturated solutions of various chemicals was used in part of the work. By means of a filter pump in each cabinet a stream of air was first pulled through the solutions and then through the glass tubes containing grasshoppers or eggs. By arranging the tubes and bottles of solutions in a series, running from the lowest to the highest humidity, one stream of air could be used for the whole series. The actual humidity in any tube in the series could be determined by replacing it with a tube of similar size containing small wet and dry bulb thermometers and allowing the stream of air to flow over the wet bulb. The following solutions were used:

Lithium chloride gave approximately 20 per cent relative humidity.

Copper nitrate gave approximately 40 per cent relative humidity.

Aluminum chloride gave approximately 50 per cent relative humidity.

Sodium chloride gave approximately 70 per cent relative humidity.

Distilled water gave approximately 97 per cent relative humidity.

This method was not entirely satisfactory, the chemicals frequently becoming so thickly crusted on the glass tubes as to stop the flow of air. The use of lithium chloride at 37° C. proved disastrous, free chlorine being liberated which killed all grasshoppers with which it came in contact.

For work with eggs constant humidities were obtained by using solutions of sulphuric acid and distilled water in closed jars. The following solutions were used:

Per cent of sulphuric acid by weight	Specific gravity of solution	Resulting humidity
67.4	1.58	10 per cent
58.7	1.49	20 " "
53.1	1.43	30 " "
48.1	1.385	40 " "
43.5	1.335	50 " "
39.9	1.300	60 " "
34.0	1.255	70 " "
27.0	1.195	80 " "
17.0	1.135	90 " "
0	1.000	100 " "

In the work done at Minnesota, constant humidities were obtained in experiments of short duration by using a Carrier Air Conditioning Cabinet. If it were possible to have a number of these cabinets this would be the ideal method of conducting experiments at constant humidities, but the expense involved is beyond the limits of most institutional budgets.

INFLUENCE OF TEMPERATURE UPON EGGS

EFFECT OF TEMPERATURE UPON RATE OF DEVELOPMENT

Rate of Egg Development at Constant Temperatures from the Time Eggs Were Laid

The first experimental work undertaken with grasshopper eggs was to determine their rate of development when placed at constant high temperatures immediately after they were laid. "Rate of development" as used in this paper is expressed as the percentage of total development of any stage accomplished in one 24-hour day. Thus if 10 days are required to complete the egg stage at any given temperature, the rate of development at that temperature would be 10 per cent of total development per day. On this basis, rates of development at various temperatures and for various sets of conditions can be compared directly without resorting to "temperature coefficients," "thermal constants," or "developmental units," all of which assume a definite knowledge of the character of the "rate-temperature"

and "time-temperature" curves for insect growth, a subject upon which many prominent biologists do not agree.

Eggs of *M. mexicanus* placed in moist sand the day they were laid required from 36 to 213 days to hatch at a constant temperature of 22° C., the average time for all egg pods being 147 days. At 27° C. the time necessary to hatch varied from 23 to 32 days, with an average of 26 days; at 32° C., from 21 to 55 days, with an average of 32 days; at 37° C., from 23 to 92 days, with an average of 46 days. The records on which these averages are based are shown in Tables 1 to 4. Length of

TABLE 1.—Length of the egg stage of M. mexicanus at a constant temperature of 22° C. from the time eggs were laid. Each record is for one egg pod containing from 15 to 25 eggs. Egg pods were kept in moist sand.

Female number	Days to hatch at 22° C.	Average
80	40 (1); 43 (1); 86 (1); 88 (1); 96 (1); 102 (1); 104 (1); 105 (1); 108 (1); 112 (1); 120 (1); 128 (1); 130 (1)	97
186	145 (1); 153 (1); 164 (1); 173 (1); 184 (1); 186 (1); 188 (1); 174 (1); 178 (1); 196 (1)	182
39	43 (1); 154 (1); 157 (1); 158 (1); 164 (1); 167 (1); 171 (1)	147
41	40 (1); 44 (1); 155 (1); 173 (1); 191 (1); 192 (1)	132
44	49 (2); 109 (3); 136 (1); 139 (1)	100
46	44 (1); 105 (1); 174 (1); 176 (1); 209 (1)	142
94	47 (1); 142 (2); 146 (1); 155 (1); 157 (2) 159 (1); 161 (1); 188 (1)	145
193	174 (1); 178 (1); 196 (1)	182
42	36 (1); 39 (2); 41 (5); 107 (1); 114 (1); 135 (1); 142 (1); 145 (3); 146 (3); 148 (2); 149 (4); 161 (1)	110
142	84 (1); 95 (5); 113 (1); 115 (1); 117 (1); 123 (1); 129 (1); 134 (1); 139 (1); 151 (2); 158 (2); 165 (1)	123
164	85 (5); 103 (1); 104 (1); 109 (1); 117 (1); 127 (1); 133 (1); 142 (1); 149 (1); 151 (1); 155 (1); 173 (1)	118
168	105 (1); 126 (2); 134 (1); 144 (1); 148 (1); 150 (1); 153 (2)	137
169	131 (1); 134 (1); 139 (1); 145 (1); 147 (1); 169 (1); 173 (1); 182 (2); 203 (1); 208 (1)	165
173	134 (6)	134
175	156 (2); 160 (1); 172 (1); 178 (1); 182 (1)	166
176	130 (1); 145 (1); 148 (1); 149 (1); 151 (2); 152 (1); 159 (1); 163 (1); 166 (3); 167 (1)	155
194	140 (1); 146 (1); 161 (2); 168 (1)	155
38	45 (1); 49 (1); 74 (1); 80 (1); 112 (1); 114 (1); 126 (1); 130 (1); 136 (1); 140 (1)	101
95	76 (1); 153 (1); 158 (1); 170 (1); 171 (2); 178 (1); 180 (1); 184 (1); 185 (1); 193 (1); 211 (1)	169
192	180 (1); 198 (1); 212 (1); 213 (1)	201
198	195 (7); 196 (2)	195
199	195 (4); 196 (1)	195
	Average of all pods	147±2.0 days
	Per cent development per day	0.68

TABLE 2.—Length of the egg stage of M. mexicanus at a constant temperature of 27° C. from the time eggs were laid. Each record is for one egg pod containing from 15 to 25 eggs. Egg pods were kept in moist sand.

Female number	Days to hatch at 27° C.	Average
28	28 (9); 32 (1)	28
29	24 (6); 25 (1); 30 (1)	25
30	24 (7); 30 (1); 33 (1)	26
31	23 (6); 25 (1); 27 (1)	24
32	26 (8); 27 (2)	26
33	24 (5); 25 (1); 28 (1)	25
34	26 (5); 35 (1)	27
35	24 (7); 25 (2)	24
36	26 (5); 29 (1)	27
37	25 (7); 32 (1)	26
40	26 (10); 27 (1); 33 (1)	27
43	27 (6); 28 (2)	27
166	23 (6); 24 (3); 26 (1)	24
200	24 (7); (26 (2); 28 (2)	25
201	24 (5); 25 (1); 26 (3); 27 (1)	25
202	25 (7); 28 (1); 32 (1)	26
204	23 (5); 24 (1); 27 (1); 30 (1)	25
205	27 (8); 28 (1); 29 (1)	27
208	24 (4); 25 (3); 26 (1); 28 (1)	25
209	25 (5); 26 (2); 27 (2); 32 (2)	27
	Average for all egg pods	26 ± 0.10 days
	Per cent development per day	3.84

TABLE 3.—Length of the egg stage of M. mexicanus at a constant temperature of 32° C. from time eggs were laid. Each record is for one egg pod containing from 15 to 25 eggs. Egg pods were kept in moist sand.

Female number	Days to hatch at 32° C.	Average
17	30 (5); 34 (1); 36 (1); 37 (1); 48 (1)	34
18	38 (3); 39 (1)	38
19	30 (7); 35 (2)	31
20	21 (6); 29 (1); 34 (1); 40 (1)	25
21	37 (5); 51 (1)	39
22	34 (2); 35 (3); 39 (2); 42 (1); 45 (1) 48 (1); 51 (2); 52 (2)	42
23	32 (11); 33 (2)	32
24	19 (2); 27 (2); 28 (1)	22
25	42 (5); 43 (1)	42
26	21 (2); 23 (3); 54 (1)	27
27	27 (5); 28 (1); 48 (1)	30
197	31 (5); 32 (1)	31
193	32 (7); 41 (1); 44 (1)	34
203	29 (3); 38 (2); 41 (1)	34
204	41 (5); 46 (3); 55 (2)	45
205	38 (9); 39 (1)	38
206	36 (10)	36
207	22 (5); 23 (2)	22
208	23 (6); 25 (1); 26 (1)	24
209	21 (7); 22 (3); 23 (1)	21
	Average for all egg pods	32 ± 0.31 days
	Per cent development per day	3.13

TABLE 4.—Length of the egg stage of M. mexicanus at a constant temperature of 37° C. from time eggs were laid. Each record is for one egg pod containing from 15 to 25 eggs. Egg pods were kept in moist sand.

Female number	Days to hatch at 37° C.	Average
5	31 (5); 43 (1); 46 (1)	35
6	37 (6); 38 (2); 60 (1)	40
8	39 (3); 53 (2)	44
9	54 (7); 55 (2)	54
10	50 (2); 56 (2); 57 (1)	54
46	23 (2); 34 (2); 35 (1); 41 (1)	32
48	40 (4); 49 (1); 61 (1)	45
65	48 (5); 67 (1)	51
69	55 (6); 63 (1)	56
73	45 (5); 59 (1)	47
83	45 (5); 46 (1); 50 (1); 54 (2)	47
88	36 (7); 45 (1); 46 (1); 50 (1); 63 (1); 86 (2)	48
98	68 (3)	68
99	36 (8); 42 (1); 44 (1); 49 (2); 69 (1)	42
100	51 (6); 79 (1); 92 (1)	59
104	29 (4); 31 (2)	29
167	51 (1); 58 (1); 65 (1); 66 (3); 70 (3); 75 (1); 84 (1)	67
176	31 (2); 33 (1); 35 (3)	33
177	37 (7); 52 (1)	39
178	41 (5); 42 (2)	41
181	41 (4); 42 (1); 43 (1)	41
	Average for all egg pods	46±0.7 days
	Per cent development per day	2.17

the egg stage and rate of development are shown graphically in Figure 1. Each record is for one egg pod containing from 15 to 25 eggs.

The average time for each pod is the weighted average of the individual eggs in the pod. Eggs at 27° C. hatched in the shortest time and with the least variation, all of the viable eggs hatching within a few days after hatching had once begun. At 22° C. there was a wide variation, eggs in the same pod often hatching intermittently over a period of several months. At 32° and 37° C. the variation in time of hatching was greater than at 27° C. but not so much as at 22° C.

Rate of Egg Development at Constant Temperatures After Exposure to Low Temperature Immediately After They Were Laid

Eggs of *M. mexicanus* placed at 0° C. (below developmental zero) immediately after they were laid and later placed at constant temperatures of 27°, 32°, and 37° C. developed more

Length of egg stage of Melanoplus mexicanus and percentage of total embryonic development per day at constant temperatures of 22°, 27°, 32° and 37° Centigrade. Eggs placed in moist sand at above temperatures the same day they were laid.
Egg Stage 147 days
% Total dev per day .68
22°C.
Egg Stage 26 days
% Total dev per day 3.84
27°C.
Egg Stage 32 days
% Total dev per day 3.13
32°C.
Egg Stage 46 days
% Total dev per day 2.17
37°C.

Figure 1

rapidly than when placed directly at these temperatures. The data for this experiment are shown in Tables 5 to 7, and the results are shown graphically in Figures 2 and 3.

"Percentage of increase in rate of development" is used to designate the amount of acceleration. The percentages listed under this heading were obtained by dividing the increase in

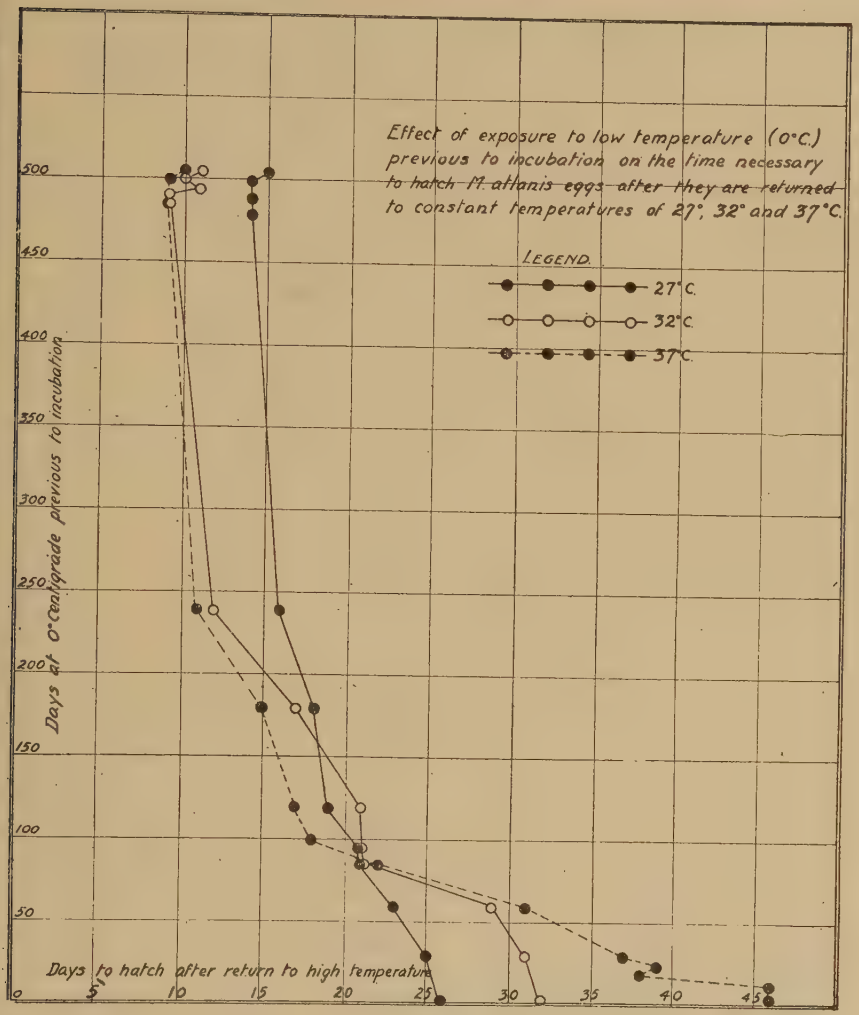

Figure 2

percentage of total development per day due to exposure to low temperature, by the percentage of total development per day without exposure to low temperature. Thus in Table 5, following an exposure of 498 days at 0° C., eggs hatched at 27° C. in 11 days, or in other words, developed at the rate of 9.09 per cent of total development in one day, an increase of 5.25 over the rate of 3.84 per cent of total development per day when

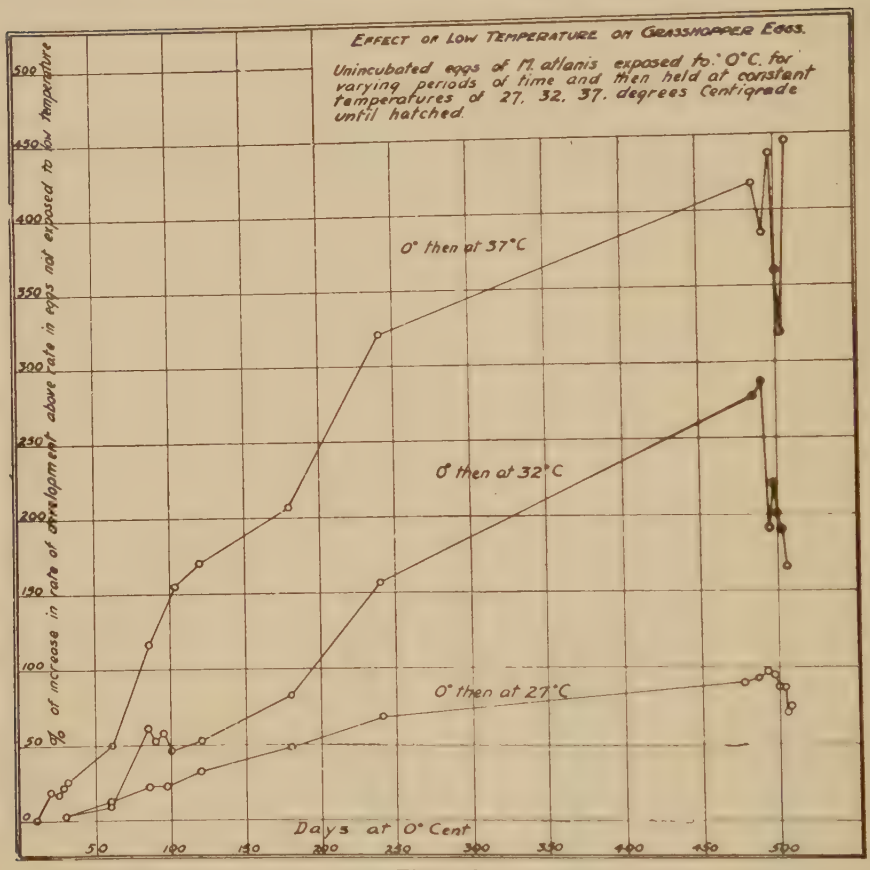
Effect of Low Temperature on Grasshopper Eggs.
Unincubated eggs of M. atlanis exposed to 0°C. for varying periods of time and then held at constant temperatures of 27, 32, 37, degrees Centigrade until hatched.
% of increase in rate of development above rate in eggs not exposed to low temperature
0° then at 37°C
0° then at 32°C
0° then at 27°C
Days at 0° Cent
50
100
150
200
250
300
350
400
450
500

Figure 3

eggs were kept at 27° C. from the time they were laid. Dividing 5.25 by 3.84 gives a ratio of 1.367, or an increase in rate of development of 136.7 per cent.

Acceleration in rate of development following exposure to low temperature varied directly with the constant high temperature to which the eggs were returned. Thus at 27°, 32°, and 37° C. the largest accelerations obtained were respectively 136.7, 357.5 and 558 per cent, while the average accelerations for these three temperatures were 66.3, 136.9, and 212.2 per cent. An exposure to 0° C. of approximately 500 days (average of all records from 493 to 507 days) gave an average accelera-

TABLE 5.—Rate of development of **M. mexicanus eggs** at a constant temperature of 27° C. after exposure to temperature below developmental zero, as compared with the rate at the same constant high temperature from the time eggs were laid. Eggs placed at 0° C. the same day they were laid. Each record is for one egg pod containing 15 to 25 eggs.

Eggs placed at 0° C. on day laid			Then at 27° until hatched				
			Days to hatch and % of total development per day				
			Theoretical		Actual		
Days at 0° C.	% of egg development at 0° C.	% of egg development at 27° C.	*Days	% Dev.	Days	% Dev.	Percentage of increase in rate of development
30	0	100	26	3.84	26	3.84	0.0
30	0	100	26	3.84	25	4.00	4.1
30	0	100	26	3.84	24	4.16	8.3
60	0	100	26	3.84	23	4.34	13.0
60	0	100	26	3.84	24	4.16	8.3
60	0	100	26	3.84	22	4.54	18.2
85	0	100	26	3.84	21	4.76	23.9
97	0	100	26	3.84	21	4.76	23.9
120	0	100	26	3.84	20	5.00	30.2
120	0	100	26	3.84	19	5.26	36.9
180	0	100	26	3.84	17	5.88	53.1
180	0	100	26	3.84	18	5.55	44.5
240	0	100	26	3.84	15	6.66	73.5
240	0	100	26	3.84	16	6.25	62.8
478	0	100	26	3.84	16	6.25	62.8
478	0	100	26	3.84	12	8.33	116.9
489	0	100	26	3.84	14	7.14	85.9
489	0	100	26	3.84	13	7.69	100.0
493	0	100	26	3.84	15	6.66	73.5
493	0	100	26	3.84	12	8.33	116.9
496	0	100	26	3.84	13	7.69	100.0
496	0	100	26	3.84	16	6.25	62.8
498	0	100	26	3.84	13	7.69	100.0
498	0	100	26	3.84	16	6.25	62.8
498	0	100	26	3.84	11	9.09	136.7
498	0	100	26	3.84	14	7.14	85.9
500	0	100	26	3.84	16	6.25	62.8
500	0	100	26	3.84	13	7.69	100.0
502	0	100	26	3.84	13	7.69	100.0
503	0	100	26	3.84	15	6.66	73.5
503	0	100	26	3.84	13	7.69	100.0
505	0	100	26	3.84	16	6.25	62.8
505	0	100	26	3.84	16	6.25	62.8
505	0	100	26	3.84	17	5.88	53.1
505	0	100	26	3.84	13	7.69	100.0
507	0	100	26	3.84	15	6.66	73.5
507	0	100	26	3.84	13	7.69	100.0
507	0	100	26	3.84	16	6.25	62.8
507	0	100	26	3.84	16	6.25	62.8

* Computed on basis of 3.84 per cent of total egg development per day which is the rate at a constant temperature of 27° C. when eggs are kept at this temperature from the time they are laid. (See Table 2.)

TABLE 6.—Rate of development of **M. mexicanus** eggs at a constant temperature of 32° C. after exposure to temperature below the developmental zero, as compared with the rate at constant high temperature from the time eggs were laid. Eggs placd at 0° C. the same day as laid. Each record is for one egg pod containing 15 to 25 eggs.

Eggs placed at 0° C. on day laid			Then at 32° until hatched				
			Days to hatch and % of total development per day				
			Theoretical		Actual		Percentage of increase in rate of development
Days at 0° C.	% of egg development at 0° C.	% of egg development at 32° C.	*Days	% Dev.	Days	% Dev.	
30	0	100	32	3.12	31	3.22	3.20
30	0	100	32	3.12	30	3.33	6.73
30	0	100	32	3.12	32	3.12	
60	0	100	32	3.12	30	3.33	6.73
60	0	100	32	3.12	29	3.44	10.25
60	0	100	32	3.12	28	3.57	14.4
84	0	100	32	3.12	19	5.26	68.5
85	0	100	32	3.12	21	4.76	52.5
88	0	100	32	3.12	22	4.54	45.5
90	0	100	32	3.12	20	5.00	60.2
90	0	100	32	3.12	22	4.54	45.5
95	0	100	32	3.12	19	5.26	68.5
95	0	100	32	3.12	22	4.54	45.5
100	0	100	32	3.12	22	4.54	45.5
120	0	100	32	3.12	22	4.54	45.5
120	0	100	32	3.12	20	5.00	60.2
180	0	100	32	3.12	18	5.55	77.9
180	0	100	32	3.12	17	5.88	88.4
240	0	100	32	3.12	12	8.33	166.9
240	0	100	32	3.12	13	7.69	146.1
486	0	100	32	3.12	9	11.11	256.
486	0	100	32	3.12	8	12.50	301.
489	0	100	32	3.12	7	14.28	357.5
489	0	100	32	3.12	10	10.00	220.
493	0	100	32	3.12	11	9.09	191.
493	0	100	32	3.12	12	8.33	166.9
493	0	100	32	3.12	10	10.00	220.
493	0	100	32	3.12	11	9.09	191.
496	0	100	32	3.12	11	9.09	191.
498	0	100	32	3.12	10	10.00	220.
498	0	100	32	3.12	10	10.00	220.
500	0	100	32	3.12	11	9.09	191.
500	0	100	32	3.12	10	10.00	220.
500	0	100	32	3.12	11	9.09	191.
501	0	100	32	3.12	9	11.11	256.
503	0	100	32	3.12	10	10.00	220.
503	0	100	32	3.12	12	8.33	166.9
503	0	100	32	3.12	11	9.09	191.
505	0	100	32	3.12	12	8.33	166.9

* Computed on the basis of 3.12 per cent of total development per day which is the rate at a constant temperature of 32° C. when eggs are kept at this temperature from the time they are laid. (See Table 3.)

tion of 83 per cent at 27° C., 200 per cent at 32° C., and 378 per cent at 37° C.

Acceleration at all three temperatures increased quite uniformly as the length of the exposure to low temperatures was increased until a period of 240 days was reached. Extending the period of exposure from 240 to approximately 500 days resulted in only slightly increased acceleration. The accelerations at all three temperatures following a 240-day exposure to

TABLE 7.—Rate of development of M. mexicanus eggs at a constant temperature of 37° C. after exposure to temperature below the developmental zero, as compared with the rate at the same constant high temperature from the time eggs are laid. Eggs placed at 0° C. the same day they were laid. Each record is for one egg pod containing 15 to 25 eggs.

Eggs placed at 0° C. on day laid			Then at 37° until hatched				
			Days to hatch and % of total development per day				
			Theoretical		Actual		Percentage of increase in rate of development
Days at 0° C.	% of egg development at 0° C.	% of egg development at 37° C.	*Days	% Dev.	Days	% Dev.	
10	0	100	46	2.17	46	2.17	.0
10	0	100	46	2.17	46	2.17	.0
20	0	100	46	2.17	38	2.63	21.2
26	0	100	46	2.17	39	2.56	17.9
28	0	100	46	2.17	38	2.63	21.2
30	0	100	46	2.17	36	2.77	27.6
30	0	100	46	2.17	38	2.63	21.2
30	0	100	46	2.17	36	2.77	27.6
60	0	100	46	2.17	32	3.12	43.7
60	0	100	46	2.17	30	3.33	53.4
60	0	100	46	2.17	30	3.33	53.4
84	0	100	46	2.17	24	4.16	91.6
86	0	100	46	2.17	19	5.26	142.0
102	0	100	46	2.17	18	5.55	155.7
120	0	100	46	2.17	17	5.88	171.0
120	0	100	46	2.17	17	5.88	171.0
180	0	100	46	2.17	16	6.25	188.0
180	0	100	46	2.17	14	7.14	229.0
240	0	100	46	2.17	10	10.00	361.0
240	0	100	46	2.17	12	8.33	284.0
486	0	100	46	2.17	10	10.00	361.0
486	0	100	46	2.17	8	12.50	476.0
493	0	100	46	2.17	9	11.11	411.0
493	0	100	46	2.17	10	10.00	361.0
498	0	100	46	2.17	11	9.09	319.0
498	0	100	46	2.17	7	14.28	558.0
500	0	100	46	2.17	10	10.00	361.0
503	0	100	46	2.17	11	9.09	319.0
507	0	100	46	2.17	12	8.33	284.0
507	0	100	46	2.17	9	11.11	411.0

* Computed on the basis of 2.17 per cent of total egg development per day which is the rate at a constant temperature of 37° C. when eggs are kept at this temperature from the time they are laid. (See Table 4.)

low temperatures were as great as some of the individual records for exposures of approximately 500 days, and only slightly below the average of all records from 478 to 507 days. Extending the length of exposure from 478 to 507 days gave no definite increase in acceleration at any temperature, indicating that maximum acceleration had already been attained. It may therefore be concluded that the length of exposure at 0° C. necessary to produce maximum acceleration is somewhere between 240 and 478 days, with the probability that an exposure of 300 days will come very close to producing maximum acceleration.

Rate of Egg Development at Constant Temperatures After Partially Developed Eggs Have Been Exposed to Low Temperatures

In the first experiment under this heading, eggs of *M. mexicanus* were placed at 22° C. as soon as laid, and allowed to develop for varying periods of time. The percentage of total development of each egg pod at 22° C. was computed on the basis of 0.68 per cent development per day, which was determined experimentally as shown in Table 1. After partial development at 22° C. had taken place, the eggs were placed at 8° C., which is below developmental zero, and later returned to constant temperatures of 27°, 32°, and 37° C. The percentage of total development at the high constant temperature was obtained by subtracting the percentage of total development at 22° C. from 100. The theoretical number of days to hatch was obtained by dividing the percentage of total development remaining by the percentage of total development per day as determined experimentally when eggs were placed at constant high temperatures immediately after they were laid. The increase in the percentage of total development per day expressed on a percentage basis was used as a measure of acceleration in the same manner as in the previous experiment.

The results of the experiment are shown in Table 8.

The acceleration in rate of development was similar to that obtained by holding undeveloped eggs at 0° C. for longer periods, and varied in the same way according to the constant high temperature to which the eggs were returned. Thus the average acceleration at 27° C. in this experiment was 71.6 per cent as compared with 83 per cent at the same temperature after ex-

TABLE 8.—Rate of development of **M. mexicanus** eggs at constant temperatures of 27°, 32°, and 37° C. after exposure to temperature below developmental zero, as compared with the rate at constant high temperatures from the time eggs were laid. Eggs allowed to partially develop at 22° C. and then held for varying periods at 8° C. Each record is for one egg pod containing 15 to 25 eggs.

Eggs placed at 22° C. on day laid		Then at 8° C. (No development)		Then at 37° until hatched				
				Days to hatch and % of total development per day				
				Theoretical		Actual		Percentage of increase in rate of development
Days at 22° C.	* % of egg development at 22° C.	Days at 8° C.	% of egg development at high temperatures	*Days	% Dev.	Days	% Dev.	
19	12.9	30	87.1	40	2.17	8	10.88	400.0
13	8.8	20	91.2	42	2.17	12	7.60	250.0
10	6.8	60	93.2	43	2.17	7	13.31	514.0
7	4.75	40	95.3	44	2.17	14	6.80	213.5
7	4.75	80	95.3	44	2.17	13	7.33	238.0
6	4.1	30	95.9	44	2.17	15	6.39	194.4
6	4.1	50	95.9	44	2.17	14	6.85	215.2
							Average	289.5
				Then at 32° C. until hatched				
48	32.6	30	67.4	20	3.13	4	16.85	422.0
39	26.5	30	73.5	23	3.13	6	12.25	291.0
34	23.1	30	76.9	25	3.13	10	7.69	145.8
32	21.7	30	78.3	25	3.13	6	13.05	316.5
32	21.7	30	78.3	25	3.13	5	15.65	400.0
30	20.4	30	79.6	25	3.13	7	11.37	262.8
29	19.7	30	80.3	26	3.13	6	13.38	327.2
28	19.0	50	81.0	26	3.13	5	16.20	417.0
27	18.4	30	81.6	26	3.13	8	10.10	225.6
25	17.0	30	83.0	27	3.13	8	10.37	231.0
25	17.0	30	83.0	27	3.13	6	13.83	341.6
25	17.0	30	83.0	27	3.13	6	13.82	341.6
23	15.6	30	84.4	27	3.13	8	10.55	236.8
23	15.6	30	84.4	27	3.13	7	12.05	284.6
19	12.9	30	87.1	28	3.13	7	12.44	297.0
15	10.2	30	89.8	29	3.13	11	8.16	160.4
14	9.5	30	91.5	29	3.13	9	10.16	224.2
14	9.5	40	91.5	29	3.13	10	9.15	192.1
7	4.7	20	95.3	30	3.13	15	6.35	102.8
7	4.7	20	95.3	30	3.13	16	5.95	90.1
7	4.7	40	95.3	30	3.13	13	7.33	134.0
7	4.7	90	95.3	30	3.13	12	7.94	153.7
							Average	254.4
				Then at 27° C. until hatched				
34	23.1	20	76.9	20	3.84	10	7.69	100.0
28	19.0	60	81.0	21	3.84	10	8.10	111.0
14	9.5	20	91.5	24	3.84	16	5.71	48.7
7	4.7	30	95.3	25	3.84	18	5.29	37.7
7	4.7	60	95.3	25	3.84	16	5.95	54.9
7	4.7	90	95.3	25	3.84	14	6.80	77.1
							Average	71.6

* Computed on the basis of 0.68, 3.84, 3.13 and 2.17 per cent of total egg development per day, which are the respective rates at constant temperatures of 22°, 27°, 32° and 37° C. when eggs are kept at these temperatures from the time they are laid. (See Tables 1-4.)

posure to 0° C. for approximately 500 days; at 32° C., 254.4 per cent as compared with 200 per cent; at 37° C., 289.5 per cent as compared with 378 per cent. There was a marked difference, however, in the length of exposure at low temperature necessary to produce maximum acceleration, partially developed eggs receiving maximum acceleration after an exposure of 60 days, while undeveloped eggs required exposures of approximately 300 days.

A second similar experiment was conducted to determine whether an exposure to a still lower temperature would yield results different from those outlined in the first experiment. Eggs were allowed to partially develop at 22° C. and then held at 0° C. instead of at 8° C. before they were returned to the constant high temperature. The results are shown in Table 9.

TABLE 9.—Rate of development of M. mexicanus eggs at a constant temperature of 32° C. after exposure to temperature below developmental zero, as compared with the rate at constant high temperatures from the time eggs were laid. Eggs allowed to partially develop at 22° C. and then held at 0° C. Each record is for one egg pod containing 15 to 25 eggs.

Eggs placed at 22° C. on day laid		Then at 0° C. (No development)		Then at 32° until hatched				
				Days to hatch and % of total development per day				Percentage of increase in rate of development
				Theoretical		Actual		
Days at 22° C.	% of egg development at 22° C.	Days at 0° C.	% of egg development at 32° C.	Days	% Dev.	Days	% Dev.	
48	32.6	30	67.4	21	3.13	3	22.46	618.0
44	29.9	30	70.1	22	3.13	5	14.02	347.4
42	28.5	30	71.5	23	3.13	4	17.87	471.0
40	27.2	30	72.8	23	3.13	4	18.20	480.5
36	24.5	30	75.5	24	3.13	5	15.10	382.0
30	20.4	30	79.6	25	3.13	5	15.92	408.0
29	19.8	30	80.2	25	3.13	5	16.04	412.8
27	18.4	30	81.6	26	3.13	5	16.32	420.5
25	17.0	30	83.0	26	3.13	5	16.60	430.0
25	17.0	30	83.0	26	3.13	7	11.85	278.4
21	14.3	30	85.7	27	3.13	7	12.24	291.0
21	14.3	30	85.7	27	3.13	8	10.11	242.0
13	8.8	30	91.2	29	3.13	13	7.01	123.9
							Average	377.4

Only one high temperature (32° C.) was used, but the comparison with the results secured in the first experiment at the same temperature shows that exposures to 0° C. resulted in greater acceleration than exposures to 8° C., the average acceleration at 32° C. following exposure to 8° C., being 254.5 per cent, while after exposure to 0° C. it was 377.4 per cent.

In Figure 4 all records of 30-day exposures to 0° C. and 8° C., followed by a return to a constant temperature of 32° C., have been included, acceleration being plotted against percentage of total development before exposure to low temperature. A glance at this graph also shows that exposure to 0° C. for the same length of time and at approximately the same stage of egg development, resulted in a greater acceleration than exposure to 8° C. This is rather significant since it presents a strong argument against the contention that might be raised, that the apparent increase in rate of development following exposures to low temperatures is not really an acceleration but instead may be caused by some egg development continuing at temperatures usually considered below the developmental zero. Of course, there is a possibility that the embryo may develop to a slight extent at 8° C. even though hatching would never take place at this temperature, but if acceleration is to be explained on this basis we would naturally expect more development to take place at 8° C. than at 0° C., and a correspondingly less time necessary to hatch when returned to constant high temperature. Instead, the reverse was found to be true, indicating that exposure to low temperature results in a real acceleration.

The same graph shows that the percentage of total development attained by the eggs before they are exposed to low temperature in the case of 30-day exposure, has a direct relationship to the degree of acceleration attained, acceleration steadily increasing up to the point where they had gone through 32.6 per cent of their total development before exposure. Experiments with eggs of more advanced development were not conducted and no conclusions can be drawn as to the stage of development at which the increase in acceleration ceases.

Bodine (2) has also noted the accelerated development of grasshopper eggs at high temperatures after exposure to low temperature. He states that with *Melanoplus differentialis,* the species used most extensively in his experiment, eggs must be allowed to partially develop before exposure to low temperatures can be tolerated for reasonably long periods and an accelerative effect at subsequent high temperature can be produced. The minimum period of initial development is placed at approximately two weeks at a temperature of 20° C. It has

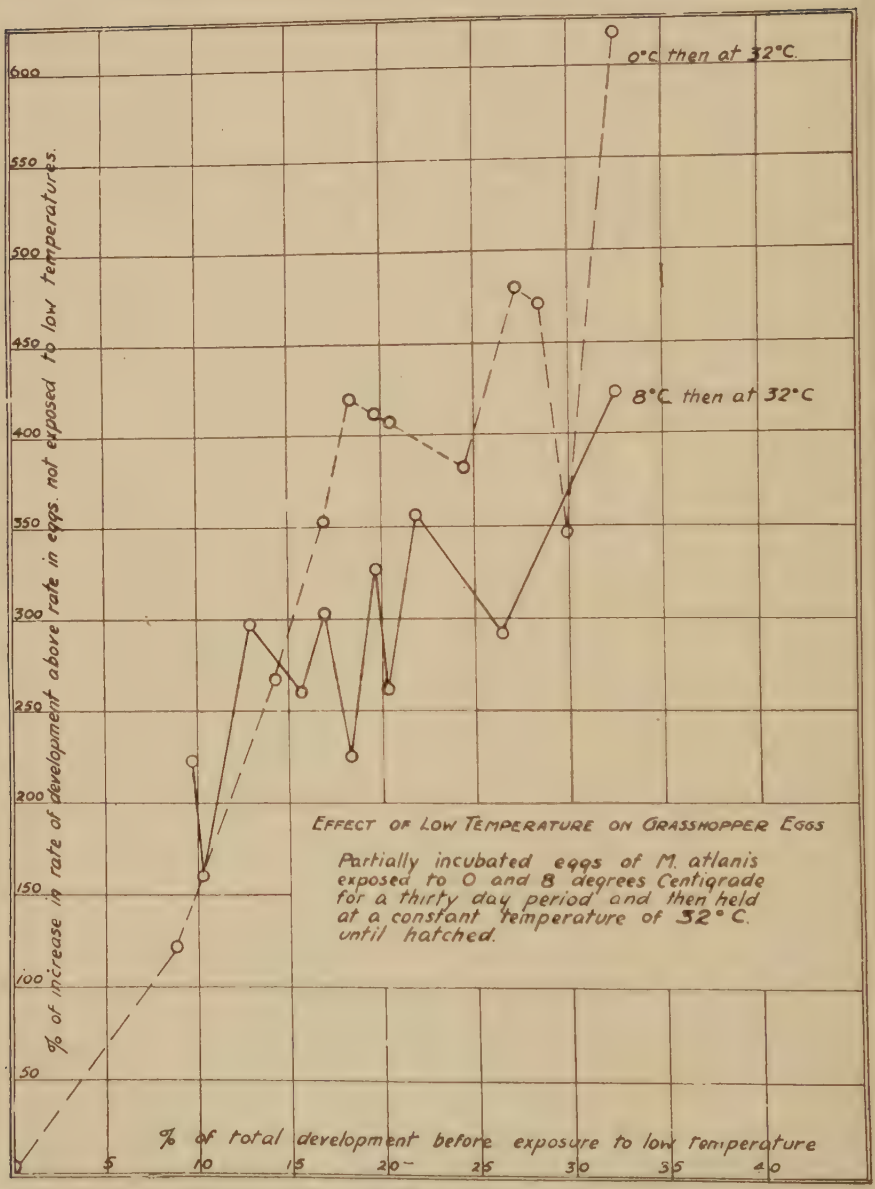
0°C then at 32°C.
8°C then at 32°C
% of increase in rate of development above rate in eggs not exposed to low temperatures.
600
550
500
450
400
350
300
250
200
150
100
50
% of total development before exposure to low temperature
5
10
15
20
25
30
35
40
EFFECT OF LOW TEMPERATURE ON GRASSHOPPER EGGS
Partially incubated eggs of M. atlanis exposed to 0 and 8 degrees Centigrade for a thirty day period and then held at a constant temperature of 32° C. until hatched.

Figure 4

already been shown in this paper that eggs of *M. mexicanus* do not require partial development before exposure to low temperature. Eggs placed at 0° C. the day they were laid and held at that temperature continuously for 500 days, hatched in 10 days when returned to a temperature of 37° C., while eggs kept continuously at 37° C. from the time they were laid required an average of 46 days, the acceleration in rate of development in this case being 361 per cent.

Rate of Development of Overwintered Field-Collected Eggs at Constant and Alternating Temperatures

Eggs of *M. mexicanus* and *C. pellucida,* which had passed the winter normally in the soil, were collected in April and divided into lots of 200 each. Four lots of each species of eggs were kept respectively at constant temperatures of 22°, 27°, 32°, and 37° C. for 24 hours each day; three lots were kept for 16 hours at 22° C. and at 27°, 32°, and 37° C. respectively for 8 hours daily; three lots were kept for 16 hours at 12° C. and 27°, 32°, and 37° C. respectively for 8 hours daily.

The rate of development under the three different conditions was compared on the basis of the growth rate per day or the percentage of the total remaining development accomplished in a 24-hour day. The eggs were partially developed when collected in the field, but for convenience in making comparisons the amount of further development necessary to hatch was placed at 100 per cent. The results are shown in Table 10.

In order that the data included under "alternating temperature" may be more easily analyzed, the following explanation of some of the column headings is given. "Percentage of development at constant temperature rate" for both high and low temperatures was obtained by multiplying the number of days by the percentage of development per day as given under "constant temperatures." Thus 40.9 per cent in the first line under "alternating temperatures" was obtained by multiplying 5.33 days by 7.69, which is the percentage of development per day at a constant temperature of 22° C. "Total development at constant temperature rate" is the sum of the percentages of development at the high and low temperatures. "Theoretical

TABLE 10.—Comparison of the rate of development of **M. Mexicanus** and **C. pellucida** eggs at constant and alternating temperatures. Over-wintered field-collected eggs kept at constant high temperatures until hatched. Some also held at low temperatures for 16 hours daily and at higher temperatures for 8 hours daily. 200 eggs used for each set of temperatures.

Constant temperatures				
	M. mexicanus		C. pellucida	
Temp. in ° C.	Days to hatch	% development per day	Days to hatch	% development per day
22	13	7.69	13	7.69
27	7	14.20	8	12.50
32	5	20.00	6	16.66
37	4	25.00	5	20.00

Alternating temperatures										
16 hours daily at low T. 8 hours daily at high T.	Low T.		High T.		Total % dev. at const. rate	Theoretical days to batch at const. T. *	Actual days to hatch at alternating T.	% dev. per day at const. T.	% dev. per day at alternating T.	% increase in rate of dev. at alternating temperature
	Days	% dev. at const. T. rate	Days	% dev. at const. T. rate						
M. mexicanus										
22 & 27	5.33	40.9	2.67	37.9	78.8	10.1	8	9.9	12.5	26.2
22 & 32	4.00	30.7	2.00	40.0	70.7	8.4	6	11.9	16.6	39.4
22 & 37	3.33	25.6	1.67	41.75	66.3	7.5	5	13.3	20.0	50.3
									Average	38.6
12 & 27	9.33	0	4.67	66.3	66.3	21.1	14	4.7	7.1	51.0
12 & 32	6.00	0	3.00	60.0	60.0	15.0	9	6.6	11.1	68.1
12 & 37	5.33	0	2.67	66.7	66.7	12.0	8	8.3	12.5	50.6
									Average	56.5
C. pellucida										
22 & 27	6.00	46.1	3.00	37.5	83.6	10.7	9	9.3	11.1	19.3
22 & 32	4.67	35.9	2.33	38.8	64.7	9.3	7	10.7	14.2	32.7
22 & 37	4.00	30.7	2.00	40.0	70.7	8.4	6	11.9	16.6	39.5
									Average	30.5
12 & 27	9.33	0	4.67	58.3	58.3	24.0	14	4.1	7.1	73.1
12 & 32	6.77	0	3.33	55.4	55.4	18.0	10	5.5	10.0	81.8
12 & 37	6.00	0	3.00	60.0	60.0	15.0	9	6.6	11.1	68.1
									Average	74.3

* Theoretical days to hatch at constant temperature rate $= \frac{\text{actual days to hatch at alternating t.} \times 100}{\text{total \% dev.}}$

number of days to hatch at constant temperature," x was obtained by solving the proportion—

x : actual days to hatch at alternating temperatures = 100 per cent: percentage of total development at constant temperature rate. Expressed as an equation—

$$x = \frac{\text{actual days to hatch at alternating temperature} \times 100}{\text{total \% of development at constant temperature rate}}$$

Then in line one under "alternating temperatures"

$$x = \frac{8 \times 100}{78.8} = 10.1$$

"Percentage of development per day at constant temperature" was obtained by dividing 100 by the theoretical number of days to hatch, and in like manner the percentage development per day at alternating temperatures was obtained by dividing 100 by the actual days to hatch. "Percentage of increase in rate of development at alternating temperature" is the difference between the rates of development per day at constant and alternating temperatures expressed on a percentage basis.

An examination of the data given under "alternating temperatures" shows that when eggs were kept for 16 hours each day at 22° C. and 8 hours at higher temperatures (27°, 32°, and 37° C.), both species showed an increase in the percentage of total development per day over the rate at constant temperature, the average acceleration for *M. mexicanus* being 38.6 per cent and for *C. pellucida* 30.5 per cent. The greatest acceleration was obtained when eggs were kept for 8 hours daily at 37° C. (the highest of the three temperatures used).

When eggs were kept at 12° C. (below developmental zero) for 16 hours daily and 8 hours at higher temperatures (27°, 32°, and 37° C.), a still greater acceleration was obtained, the average for *M. mexicanus* being 56.5 per cent and for *C. pellucida* 74.3 per cent. In this case the greatest acceleration in both species was obtained at 32° C. instead of at 37° C.

If the data in Table 10 are analyzed it will be noted that holding eggs for 8 hours daily at 5° higher and for 16 hours at 5° lower than any given constant temperature or set of alternating temperatures, will give approximately the same amount of total development per day as when held at the original temperature. In the one instance where data were available the

same condition was also found to hold true for a spread of 10 degrees in temperature. This relation can be more easily seen by bringing together all the data in which the spread in temperature was either 5 or 10 degrees above the original temperature for 8 hours and 5 to 10 degrees below for 16 hours daily. It was assumed that no appreciable development took place below 17° C. and the alternating temperatures of 12° and 27° C. were therefore considered as a 5° spread each way from 22° C.

Temperature ° C.	Days to hatch		Per cent development per day	
	M. mexicanus	C. pellucida	M. mexicanus	C. pellucida
22° Constant	13	13	7.69	7.69
12° and 27° Alternating	14	14	7.10	7.10
Difference 5° C.	1	1	0.59	0.59
27° Constant	7	8	14.20	12.5
22° and 32° Alternating	6	9	16.60	14.2
Difference 5° C.	1	1	2.40	1.7
27° Constant	7	8	14.20	12.5
12° and 37° Alternating	8	9	12.50	11.1
Difference 10° C.	1	1	1.7	1.4
22° and 27° Alternating	8	9	12.5	11.1
12° and 32° Alternating	9	10	11.1	10.1
Difference 5° C.	1	1	1.4	1.
22° and 32° Alternating	6	7	16.6	14.2
12° and 37° Alternating	8	9	12.5	11.1
Difference 5° C.	2	2	4.1	3.1

Although there are not sufficient data to warrant the drawing of definite conclusions, the number of days required to hatch eggs is in every case so nearly equal that it suggests the possibility that a general principle may be involved. Since holding eggs for 8 hours at 5° higher and for 16 hours daily at 5° lower than any given temperature within the normal range of development gives approximately the same amount of development per day as when held constantly at that temperature, the principle might be roughly stated as follows: In any set of daily alternating temperatures within the range of normal development when the time spent at the low temperature is twice that at the high temperature, the percentage of development per day will be equivalent to the percentage of development per day at a constant temperature equal to the mean of the two alternating temperatures.

In nature the division of the 24-hour day into a period of fairly continuous high temperature during the middle of the day and a period of low temperature during the late afternoon, night, and early morning, corresponds rather closely to the 8-hour period of high temperature and the 16-hour period of low temperature used in the laboratory experiments. This division of temperature during the day and the principle stated above suggest a possible rough method for determining the amount of development taking place under the varying temperatures found in nature and of expressing it in constant temperature equivalents. If hourly thermograph records were available, the mean of the 8 warmest hours could be selected as the high temperature and the mean of the 16 coolest hours as the low temperature. Using the principle already stated, the amount of daily development would then be approximately the same as at a constant temperature equal to the mean of the high and low temperatures. If, for example, the mean temperature for the 8 warmest hours was 32° C. and for the 16 coolest hours was 22° C. the amount of development per day would not be equivalent to that at a constant temperature of 25.6° C., which is the weighted daily mean temperature, but instead would be equivalent to development at a constant temperature of 27° C., obtained by taking the mean of the two temperatures. If only daily maximum and minimum temperatures were available, the constant temperature at which equivalent development would take place could be obtained by giving the maximum temperatures twice the weight of the minimum temperature. Thus, if the minimum were 18° C. and the maximum 36° C., the mean of 18°, 36°, and 36° C., or 30° C., should be used instead of the daily mean temperature of 27° C.

A series of carefully conducted experiments in which development under outdoor conditions is compared with development at constant temperatures over a period of several years, should be carried out before this method of converting rates of development at varying temperatures into constant temperature equivalents can be accepted, but the data at hand at least seem to warrant suggesting it as a possibility. In another section of this paper, data on the development of grasshopper

nymphs at constant and alternating temperatures will be presented which give added weight to the principle and method suggested by the data on grasshopper eggs.

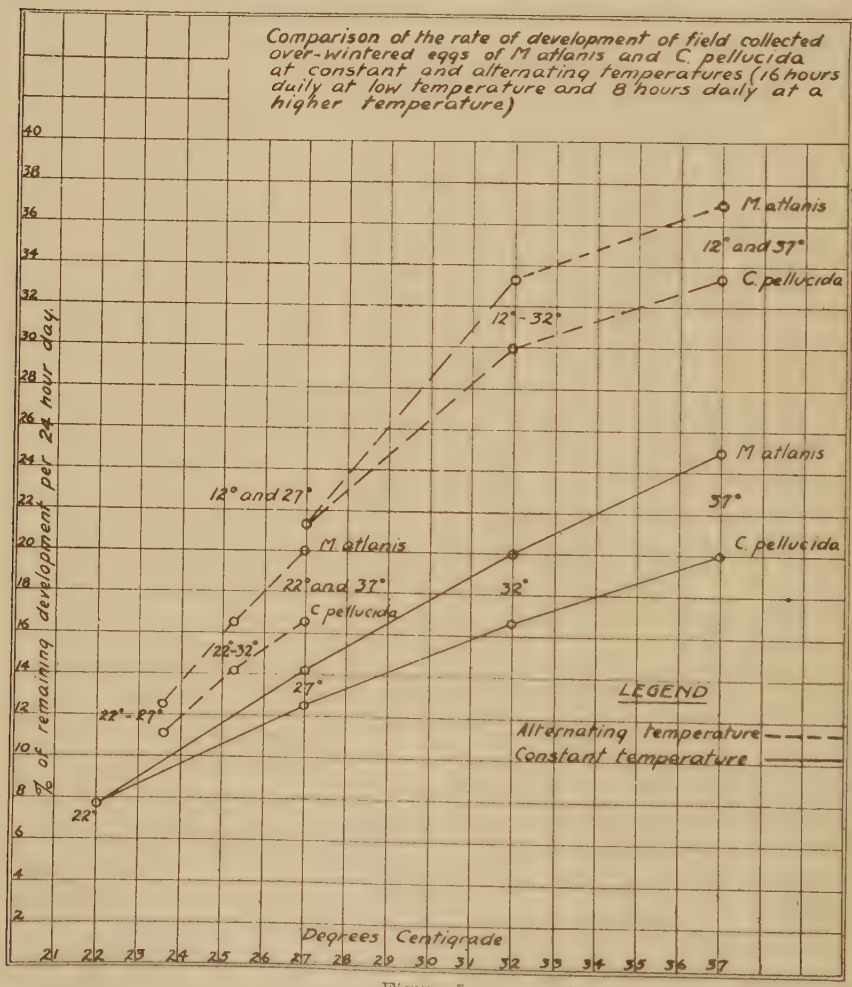

Figure 5

In Figure 5 daily growth rates or percentages of remaining development per day have been plotted against temperature for both constant and alternating temperatures. In the set of alternating temperatures where the low temperature was 22° C., which is above the developmental zero, the true daily mean tem-

perature was used in locating the three temperature points and the amount of development per day was taken from Table 10. Thus, 16 hours at 22° C. and 8 hours at 27° C. daily would result in a mean daily temperature of 23.6° C. The rate of development per day of *M. mexicanus* eggs under this set of conditions is found by consulting Table 10 to be 12.5 per cent. In the set of alternating temperatures where the low temperature was 12° C., which is below developmental zero, the percentage of development per day was computed for daily mean temperatures of 27°, 32°, and 37° C. By consulting Table 10, 16 hours at 12° C. and 8 hours at 27° C. are found to result in 7.1 per cent development per day; but since no development takes place at 12° C. it must be considered that 7.1 per cent development takes place in one-third of a day at 27° C. and the rate per day would therefore be 3×7.1 or 21.3 per cent.

When the points plotted as above are connected by straight lines, three sets of curves are obtained which are similar to the reciprocal growth curves figured by Krogh (9), Peairs (11), and other workers. The curves for alternating temperature, although showing a higher rate of development, are of the same type as those for constant temperatures, indicating that both constant and alternating temperatures are governed by the same general principles.

Discussion of the Effect of Temperature Upon Rate of Egg Development

From the data presented it is clear that there is a marked difference in the rate of development of *M. mexicanus* eggs when placed at high temperatures immediately after they are laid, as contrasted with egg development after exposure to low temperatures either before or after some development has taken place. The rate of development after such exposures to low temperatures increased directly with temperatures at all three temperatures used in the experiments—27°, 32°, and 37° C. When eggs were placed at high temperatures immediately after they were laid, very different results were obtained, development being much reduced both below and above 27° C., the point of most rapid development, the retardation at 37° C. being greater than at 32° C. Retardation in egg development at high temperatures is decidedly beneficial to *M. mexicanus*. This

grasshopper starts laying eggs in July and continues until cold weather comes in the fall. The earlier laid eggs are frequently exposed to soil temperature above 37° C., and if the rate of development increased at the higher temperature many eggs would hatch during the late summer, after there was not time to complete development and deposit eggs. Such late hatched grasshoppers would die in the fall without having reproduced. On the other hand, eggs laid during comparatively cool weather in the late summer and early fall develop faster than eggs laid earlier in the season, and as a result all eggs go into the winter at much nearer the same stage of development than would be the case if the rate of development increased directly with temperature.

It has been shown that exposure of *M. mexicanus* eggs to low temperatures results in a greatly increased rate of development when they are returned to higher temperatures. The degree of acceleration obtained in this way depends upon the amount of development before exposure, the length of the exposure, and the high temperature to which they are returned. The effect of such exposures on eggs not previously incubated is shown in Tables 1 to 4. It will be noted that after comparatively long exposures to 0° C. the difference in the average time necessary to hatch at 27° and 37° C. was only 6 days, while without such exposure it was 20 days. It is also interesting to note that without exposure to low temperatures the average time to hatch varies inversely with the temperatures of 27°, 32°, and 37° C., while after exposures to low temperatures it varies directly with these temperatures. In nature eggs are exposed to low temperatures for long periods during the winter months, which should result in an acceleration in development the following spring similar to that obtained in laboratory experiments. That such is the case is evidenced by the fact that all eggs under the same general soil moisture and temperature conditions do hatch within a very few days after general hatching has once started in the spring. Were it not for this acceleration, eggs laid late in the fall would hatch weeks, or even months, later than earlier laid eggs which had completed most of their development before exposure to winter conditions.

In the retardation of development at high temperature

during the summer, more rapid development during cool weather in the fall, and accelerated development in the spring, due to exposure to low temperature during the winter, there exists a set of factors which tends to bring about complete hatching during a few days in the spring of all eggs laid over a period of several months during the previous summer and fall. This is a distinct advantage to the species for it confines the nymphal period to the spring season when green succulent food is always available, at least during the early instars. It also brings practically all individuals to maturity at the beginning of summer and thus allows a maximum time for egg laying.

AT WHAT AIR AND SOIL TEMPERATURE DO EGGS HATCH

Lowest Air Temperature at Which Eggs Will Hatch in Constant Temperature Cabinets

Well-incubated field-collected eggs of *M. mexicanus*, which hatched in a few hours at 27° C., required 38 days to hatch at 19° C. and failed to hatch at 17°, 12°, and 7° C. after 6 months' exposure. Well-incubated *C. pellucida* eggs hatch in 30 to 40 days at 19° C. but generally fail to hatch at 17° C. even after long exposure. In one lot, however, a small percentage of eggs hatched at 17° C. in approximately 35 days. No *C. pellucida* eggs have ever been hatched at 12° and 7° C., even though several lots of eggs which hatched at 27° C. in 3 days were held at these temperatures for 6 months. A quantity of eggs of this species kept in a cold storage room which varied from 5° to 15° C. did not hatch during a period of two years, but when the temperature accidentally went to 22° C. for a few hours a large number of them hatched. Eggs placed at 7° and 12° C. and held for 500 days showed no egg spots or other indications of embryonic development that could be seen by dissection under a binocular microscope.

Developmental zero, as defined by Sanderson and Peairs, is "that point at which the insect may be kept, theoretically at least, without change for an indefinite period." From the foregoing data it may be concluded that developmental zero for both *M. mexicanus* and *C. pellucida* eggs is approximately 17° C.

Air and Soil Temperature at Which Eggs Normally Hatch in the Field

Observations based on the first appearance of nymphs in abundance in the spring and a study of weather records show that general hatching of both *M. mexicanus* and *C. pellucida* eggs takes place during the first warm period of from 3 to 5 days having maximum temperatures above approximately 24° C. (75.2° F.). A number of definite records obtained from county agents, personal observations, and from official weather records substantiate the above statement. These records are included in Table 11.

In every case the 6 days for which maximum temperatures are given include the warmest 3-day period that had occurred since the winter months. Such warm periods generally do not occur in Montana until the last two weeks in May or the first week in June, and over a long period of years general hatching of *M. mexicanus* and *C. pellucida* has rarely occurred before May 15. The last record in the table, that for Havre in 1926, shows that such warm periods may occur earlier and cause the hatching of large numbers of eggs much in advance of the normal hatching period. In the fall of 1925 eggs were extremely abundant in certain localities in the vicinity of Havre and preparations were made for an extensive control campaign the following spring. On April 14 the weather turned unseasonably warm, the maximum temperature being 26.6° C. (80° F.), and for 6 days the maximum was only once below 23.3° C. (74° F.). As a result a high percentage of the eggs hatched and the nymphs gradually died during the cool, unfavorable weather that followed. This area was visited on May 16, at which time 90 per cent of the egg pods in bare soil were found to be hatched, but in soil covered with Russian thistle or straw eggs were still unhatched. Soil temperatures indicate the reason for this difference. With an air temperature of 22.2° C. (72° F.) at 4 feet, the temperature in bare dry soil at a depth of 2 inches was 25.5° C. (78° F.); under Russian thistle in dry soil at the same depth, 18.8° C. (66° F.); and in wet soil, 16.6° C. (62° F.). Fortunately for the farmers of the region, only a small percentage of the eggs were thus protected and, as a result of the early hatching of the greater part of the eggs in April, no control campaign was necessary and crops were not materially

TABLE 11.—Maximum daily temperatures 5 days previous and at time of first general hatching of **M. mexicanus** and **C. pellucida** eggs in the spring.

Locality	Year	Max. temp. for 5 days before hatching					First general hatching	Maximum temperature	Species
		5	4	3	2	1			
Kalispell	1921	21.6° C. 71° F.	17.7 64	24.4 76	25.0 77	23.3 74	June 6	25° C. 77° F.	C. pellucida
Bozeman	1921	20° C. 68° F.	23.8 75	25.0 77	24.4 76	23.8 75	June 13	31.6° C. 89° F.	C. pellucida
Bozeman	1922	16.6° C. 62° F.	20.5 69	22.7 73	25.5 78	27.7 82	June 5	26.6° C. 80° F.	C. pellucida
Great Falls	1922	15.0° C. 59° F.	21.6 71	26.6 80	23.3 74	25.5 78	May 19	24.4° C. 76° F.	M. mexicanus
Choteau	1924	16.6° C. 62° F.	25.5 78	25.5 78	23.8 75	21.1 70	May 14	26.1° C. 79° F.	M. mexicanus
Choteau	1925	17.2° C. 63° F.	21.1 70	26.1 79	28.3 83	28.3 83	May 20	30.5° C. 87° F.	M. mexicanus
Havre	1926	23.3° C. 74° F.	13.3 56	17.2 63	26.6 80	25.0 77	April 16	26.1° C. 79° F.	M. mexicanus

damaged. Such continued warm weather in the early spring is very rare, however, and no other record of a general hatching in April has ever come to our attention in Montana.

Whenever possible observations have been made on the air and soil temperatures prevailing at the time the eggs were found hatching in the field. Air temperatures were taken by whirling a thermometer 4 feet above the ground. Soil surface temperatures were taken by placing the thermometer on the surface of the ground and barely covering the bulb with loose soil. Temperature readings were also taken 2 inches below the soil surface, since this is the depth at which egg pods are usually found. In making these readings the bulb of the thermometer was pushed into the soil to a depth of 2 inches. Air and soil temperatures prevailing at time of hatching are shown in Table 12.

TABLE 12.—Temperature prevailing at time eggs of M. mexicanus and C. pellucida were observed hatching under natural conditions.

Locality	Date	Air 4 feet		Soil surface		Soil 2 inches		Species	
Power	5/13/24	21° C.	69.8° F.	28° C.	82.4° F.	23° C.	73.4° F.	M. mexicanus	
Conrad	5/14/24	25	77	32	89.6	30	86.0	"	"
"	5/15/24	27	80.6	44	111.2	35	95.0	"	"
Valier	5/16/24	26	78.8	37	98.6	27	80.6	"	"
"	5/17/24	23	73.4	36	96.8	26	78.8	"	"
Three Forks	6/2/24	23	73.4	32	89.6	25	77.0	"	"
" "	6/3/24	24	75.2	35	95.0	30	86.0	"	"
Wilsall	5/18/25	23	73.4	40	104.0	35	95.0	"	"
"	5/19/25	22	71.6	40	104.0	33	81.4	"	"
Three Forks	5/20/25	22	71.6	30	86.0	27	80.6	"	"
Hingham	5/16/26	22	71.6	31	87.8	25	77.0	"	"
"	5/25/26	20	68.0	32	89.6	26	78.8	"	"
Bozeman	6/6/21	21	69.8	27	80.6	23	73.4	C. pellucida	
"	6/7/21	23	73.4	30	86.0	24	75.2	"	"
Kalispell	6/12/21	22	71.6	30	86.0	24	75.2	"	"
Bozeman	5/24/22	24	75.2	33	91.4	28	82.4	"	"
"	5/25/22	24	75.2	33	91.4	27	80.6	"	"
Wilsall	5/18/25	22	71.6	26	96.8	26	78.8	"	"
"	5/19/25	21	69.8	35	95.0	26	78.8	"	"

From the data presented in Table 12 it will be noted that in all cases where hatching was observed, the soil surface temperature was 27° C. (80.6° F.) or over, and the soil temperature at 2 inches was 23° C. (73.4° F.) or over. Eggs may possibly hatch at lower soil temperatures, but, as previously noted, eggs at Havre in soil covered with Russian thistle remained unhatched when the soil temperature was 18.8° C. (66° F.) while eggs in bare soil a few feet away had hatched a month before.

The lowest air temperature at which hatching was observed was 20° C. (68° F.) but the soil surface temperature at the time was 32° C. (89.6° F.), exactly the same as in another record where the air temperature was 25° C. (77° F.). Soil temperatures at the point where the eggs are placed are, of course, more important in determining the time of hatching than air temperatures, but, as just pointed out, there is not always a uniform correlation between them. Moisture, color, texture, slope, and ground covering all have an important influence on soil temperature. This often results in uneven hatching in the same locality, eggs in dry, dark soil on bare south slopes hatching earliest, while eggs in wet soil may not hatch for weeks or even months. In general, however, only a small percentage of the total number of eggs are in soil which for various reasons remains below normal in temperature, and in any one locality a very high percentage of eggs hatch during the first period of continued warm weather in the spring when maximum daily air temperatures are 24° C. (75.2° F.) or above, and soil surface temperatures 27° C. (80.6° F.) or above, and soil temperatures at 2 inches are 23° C. (73.4° F.) or above.

EFFECT OF LOW TEMPERATURE UPON VITALITY OF EGGS

Undercooling and Freezing Points

Experiments to determine the undercooling and freezing points of *M. mexicanus* and *C. pellucida* eggs were conducted by the thermoelectric method described by Taylor (19) and used more recently by Carter (4). In most of the experiments a single egg was placed in a small gelatine capsule into which the thermo-couple point was inserted and held firmly in contact with the egg but not piercing it. With some of the eggs the thermo-couple point was pushed into the egg until it was in contact with the liquid content. The temperature was gradually lowered until a pronounced "rebound" was indicated by the galvanometer. The lowest temperature reading taken before the rebound was used as the point of undercooling, and the reading taken immediately after the rebound was used as the "freezing point." The terms "undercooling" and "freezing point" are used with the meaning defined by Payne (10). "By undercooling point is meant the limiting temperature below the

freezing point of a liquid, to which it can be cooled without freezing; by freezing is meant actual crystallization of a given body fluid or tissue accompanied by the giving off of heat." The term "rebound" is used to designate the sudden fluctuation in temperature caused by the liberation of heat when freezing takes place after a liquid has been undercooled.

The results of the experiments are shown in Table 13.

Eggs of *M. mexicanus*, previously kept for a month in dry sand at a temperature of 22° C., froze at an average temperature of –19.5° C. and undercooled to an average temperature of –21.3° C. Eggs of *C. pellucida*, kept under the same conditions previous to freezing, froze at an average temperature of –15° C. and undercooled to an average temperature of –17° C., a difference of 4.5° C. in the freezing point and 4.3° C. in the undercooling point from eggs of *M. mexicanus*. Approximately the same difference existed between eggs of the same species previously kept in moist sand at 22° C. and in moist sand at a temperature of 0° to 4° C. The average difference in the freezing and undercooling points of eggs of the two species under all three sets of conditions was 4° C.

Eggs of both species previously kept for a month in moist sand at 22° C. had higher freezing and undercooling points than when kept in dry sand at the same temperature, eggs of *M. mexicanus* showing a difference of 1.7° C. in both freezing and undercooling points while with *C. pellucida* eggs there was a difference of 1.1° C. in the freezing point and 1.4° C. in the undercooling point.

Eggs previously kept for a month in moist sand at a temperature of 0° to 4° C. showed no greater cold resistance than eggs previously kept in moist sand at 22° C., the average freezing and undercooling points for the two sets of conditions being almost identical.

Eggs of both species which were punctured by pushing the thermo-couple point into the egg were strikingly less cold resistant than uninjured eggs. With *M. mexicanus*, eggs previously kept in dry sand at 22° C. froze at an average temperature of –2.4° C. when injured and at –17.7° C. when uninjured, a difference of 15.3° C. It is of interest to note that the freezing and undercooling points of injured eggs are almost identical

TABLE 13.—Undercooling and freezing points of M. mexicanus and C. pellucida eggs.

M. mexicanus				C. pellucida			
Minutes to reach undercooling point	Undercooling point ° C.	Freezing point ° C.	Previous history of eggs	Minutes to reach undercooling point	Undercooling point ° C.	Freezing point ° C.	Previous history of eggs
9	−19.5	−18.0	At 22° C.	8	−16.5	−14.5	At 22° C.
8	−20.5	−19.5	in dry	10	−16.5	−15.0	in dry
10	−23.0	−20.0	sand	5	−17.0	−14.5	sand
8	−21.5	−20.0		6	−16.0	−14.5	
7	−20.0	−18.0		7	−17.0	−15.0	
8	−24.0	−22.0		8	−18.0	−15.0	
6	−20.5	−18.5		6	−17.0	−15.0	
7	−23.0	−21.0		5	−16.5	−15.0	
8	−19.0	−18.0		6	−18.0	−15.5	
8	−22.0	−20.5		7	−18.0	−16.5	
Average	−21.3	−19.5		Average	−17.0	−15.0	
6	−18.5	−17.0	At 22° C.	8	−16.0	−14.5	At 22° C.
8	−19.0	−17.0	in moist	10	−15.0	−13.5	in moist
10	−19.5	−18.0	sand	9	−15.5	−14.0	sand
9	−20.0	−17.5		6	−16.5	−15.0	
8	−19.0	−17.5		8	−14.5	−13.0	
10	−21.0	−18.5		7	−15.0	−13.0	
7	−19.0	−17.0		7	−16.0	−14.0	
7	−20.5	−19.0		9	−15.5	−13.5	
10	−21.0	−19.0		8	−17.0	−15.0	
8	−19.0	−17.5		6	−15.0	−13.5	
Average	−19.6	−17.8		Average	−15.6	−13.9	
7	−20.0	−18.0	At 0 to	7	−15.5	−14.0	At 0 to
7	−18.5	−17.0	4° C. in	5	−16.0	−15.0	4° C. in
10	−18.0	−16.5	moist	8	−15.5	−13.5	moist
8	−19.0	−17.5	sand	7	−16.5	−15.0	sand
8	−20.5	−18.5		8	−16.0	−14.0	
8	−19.5	−17.5		6	−15.0	−13.5	
9	−20.0	−17.5		9	−15.5	−14.0	
8	−20.5	−19.0		6	−15.0	−13.0	
9	−20.0	−18.0		9	−16.5	−14.5	
7	−19.5	−17.5		8	−15.0	−13.5	
Average	−19.5	−17.7		Average	−15.6	−14.0	
5	− 5.0	− 2.0	At 22° C.	4	− 3.5	− 2.0	At 22° C.
6	− 4.0	− 2.0	in dry sand	4	− 4.0	− 2.5	in dry
4	− 5.0	− 2.5	Egg	5	− 4.5	− 3.0	sand
5	− 4.5	− 3.0	punc-	5	− 4.0	− 2.0	
4	− 4.5	− 2.5	tured	4	− 4.5	− 2.5	
Average	− 4.6	− 2.4		Average	− 4.1	− 2.4	
4	− 3.0	0.0	At 0 to 4°	5	− 3.5	0.0	At 0 to
5	− 3.5	− 0.5	C. in moist	5	− 3.0	0.0	4° C. in
5	− 4.0	0.0	sand. Egg	4	− 4.0	0.0	moist
4	− 3.5	− 0.5	punc-	4	− 3.5	0.0	sand
5	− 3.0	0.0	tured	5	− 3.0	0.0	
Average	− 3.2	− 0.2		Average	− 3.2	0.0	

with the freezing and undercooling points of newly hatched nymphs.

Injured eggs of *M. mexicanus* and *C. pellucida* froze and undercooled at approximately the same temperature, differing in this respect from uninjured eggs, in which there is a difference of approximately 4° C. between the two species. Eggs previously kept in moist sand froze at a slightly higher temperature after being injured than did eggs kept in dry sand.

Many of the eggs of both *M. mexicanus* and *C. pellucida* which were undercooled and frozen in the above experiments hatched in a few days when held at a constant temperature of 32° C., indicating that the formation of ice crystals in the eggs is not alone sufficient to kill the egg outright.

Low Temperatures Necessary to Kill Eggs

In order to determine what low temperatures were necessary to actually kill eggs, lots of 25 eggs of both *M. mexicanus* and *C. pellucida* were held at –10°, –15°, –20°, –25° and –30° C. for 16-hour periods and then held at 32° C. to see if they would hatch. The results of the experiment are shown in Table 14.

TABLE 14.—Low temperatures necessary to kill M. mexicanus and C. pellucida eggs by a sixteen-hour exposure.

Number of eggs in each lot	Low temperature to which eggs were exposed	Length of exposure	Percentage of eggs hatched at 32° C. after exposure to low temperature			
			M. mexicanus		C. pellucida	
			From dry sand	From moist sand	From dry sand	From moist sand
25	–10° C.	16 hrs	80.	76.	80.	84.
25	–15° C.	16 hrs.	80.	84.	80.	88.
25	–20° C.	16 hrs.	80.	80.	84.	80.
25	–25° C.	16 hrs.	56.	48.	36.	24.
25	–30° C.	16 hrs.	0	0	0	0
100	Room temp. (checks)	16 hrs.	79.	81.	78.	82.

Sixteen hours at –25° C. killed part of the eggs, and none survived the same exposure at –30° C. The percentage of eggs that hatched following 16-hour exposures at the higher temperatures was approximately the same as that of check lots of 100 eggs held at room temperatures. It may therefore be concluded that overnight exposure to temperatures ranging from –25° to –30° C. (–13° to –22° F.) will result in the killing of

from 50 to 100 per cent of the eggs of *M. mexicanus* and *C. pellucida.*

Do Such Low Temperatures Occur Under Field Conditions

During years of grasshopper abundance farmers frequently ask if severe winter weather will kill any of the eggs. It is therefore of some economic interest to look through available soil temperature records and find out how frequently temperatures of –13° to –22° F. have been recorded at soil depths of 2 to 4 inches, which is the approximate depth at which grasshopper eggs are found. At the Nebraska Experiment Station records for temperatures at 3 inches are available covering the period from 1894 to 1902. During this period the lowest temperature recorded was 4.5° F. (–15.8° C.) on February 11, 1899 (17). No statement is made as to whether the ground was bare or covered with snow.

Mr. H. L. Seamans, entomologist in charge for Alberta, has kept soil thermograph records at 4 inches at Lethbridge since February, 1924, and I am indebted to him for the statement that the lowest temperature recorded at that depth was 21° F. (–6.11° C.). This occurred twice—on January 28, 1926, when the air temperature was –10° F. (–23.3° C.) and on February 2, 1926, when the air temperature was –2° F. (–18.9° C.). During the time of Mr. Seamans' records, air temperatures of –45° F. (–42.8° C.) have been recorded but a covering of snow kept the soil temperature from going as low as on the dates given above.

Mr. G. A. Mail made daily records of soil temperatures at St. Paul, Minnesota, from October, 1927, to May, 1928, and at Bozeman, Montana, from October, 1928, until the present time. According to his unpublished records the lowest temperature recorded at 2 inches at St. Paul was –0.4° F. (–18° C.) on January 2, 1928. This was in bare ground and at an air temperature of –20° F. (–28.9° C.). Under a covering of 8 inches of snow the temperature at 2 inches on the same date was 30.8° F. (–0.67° C.). At Bozeman the lowest temperature recorded at 2 inches was –4° F. (–20° C.) on February 7, 1929. This was in bare ground and at an air temperature of –29° F. (–33.9° C.). Under a covering of 11 inches of snow on the

same date, the soil temperature at 2 inches was only 28.4° F. (–2° C.).

From these records it would appear that eggs covered with 2 inches of soil are in little danger of being killed, even when the ground is bare and air temperatures are as low as –29° F. (–33.9° C.). Such low temperatures are generally accompanied by snow, which brings the soil temperature far above the danger point. Eggs which have been brought to the surface by cultivation of the ground, or which have been exposed by blowing away of the soil, may occasionally be killed by the occurrence of air temperatures below –13° F. (–25° C.) when the ground is not protected by snow.

EFFECT OF HIGH TEMPERATURES UPON VITALITY OF EGGS

Experiments to determine what high temperatures were necessary to kill eggs were conducted by placing eggs in electric ovens held at constant high temperatures. Eggs of both *M. mexicanus* and *C. pellucida* were held at 45° and 50° C. for 1, 2, and 3 hours, and at 60° and 70° C. for 10, 20, and 30 minutes. Two lots of eggs were used in each exposure, one which had previously been kept in dry sand for several weeks and the other in moist sand. After exposure to high temperature the eggs were then held at constant temperature of 32° C. to determine how many would hatch. The results of the experiment are shown in Table 15.

Eggs held at 70° C. for 10 minutes or more were all killed, as were eggs held at 60° C. for 20 and 30 minutes. A few eggs survived a 10-minute exposure at 60° C. Eggs held at 50° C. for 2 and 3 hours were all killed but some survived a 1-hour exposure at this temperature. A 3-hour exposure at 45° C. killed a few eggs, but in eggs held for 1 and 2 hours at this temperature the percentage hatched was approximately the same as in a check lot of 100 eggs held at room temperature. At temperatures where the percentage of hatch was reduced but eggs were not all killed, the reduction was greater in eggs previously kept in moist sand then in eggs from dry sand.

From the foregoing it may be concluded that eggs of both species will be endangered by exposure of 3 or more hours at

TABLE 15.—High temperatures necessary to kill M. mexicanus and C. pellucida eggs.

Number of eggs in each lot	High temperature to which eggs were exposed	Length of exposure	Percentage of eggs hatched at 32° C. after exposure to high temperature			
			M. mexicanus		C. pellucida	
			From dry sand	From moist sand	From dry sand	From moist sand
25	45° C.	1 hr.	76.	80.	84.	80
25	45° C.	2 hrs.	80.	76.	76.	80.
25	45° C.	3 hrs.	68.	56.	72.	68.
50	50° C.	1 hr.	28.	16.	52.	26.5
50	50° C.	2 hrs.	0	0	0	0
50	50° C.	3 hrs.	0	0	0	0
25	60° C.	10 min.	12	8.	52.	20.
25	60° C.	20 min.	0	0	0	0
25	60° C.	30 min.	0	0	0	0
25	70° C.	10 min.	0	0	0	0
25	70° C.	20 min.	0	0	0	0
25	70° C.	30 min.	0	0	0	0
100	Room temp. (check)	16 hrs.	79.	81.	78.	82.

45° C. (113° F.) and will be killed by a 2-hour exposure at 50° C. (122° F.) or a 20-minute exposure at 60° C. (140° F.).

Do Such High Temperatures Occur Under Field Conditions

It is a well-known fact that during the summer months the ground becomes very warm and it is of interest to determine whether soil temperatures at a depth of 2 inches, about where the eggs are found, are ever high enough to affect the vitality of the eggs.

In Michigan the maximum temperature recorded (3) at a depth of 2 inches, during the summer of 1915, was 96.5° F. (35.7° C.).

In daily soil thermograph records made at Willow Creek, Montana, during the summers of 1925 and 1926, the highest recorded temperature at a depth of 2 inches was 99° F. (37.2° C.). None of these high records approaches the danger zone of 113° F. (45° C.), and it is therefore improbable that grasshopper eggs are ever killed by heat when covered to a depth of 2 inches. Eggs brought to the surface by cultivation, however, would sometimes be exposed to killing temperatures, since soil surface temperatures of 113° to 131° F. (45° to 55° C.) are not uncommon either in Montana or Minnesota.

INFLUENCE OF TEMPERATURE UPON NYMPHS AND ADULTS

EFFECT OF TEMPERATURE UPON RATE OF DEVELOPMENT

Rate of Development at Constant Temperatures

Data on the number of days in the nymphal stage of four species of grasshoppers reared at constant temperatures have accumulated over a period of several years, during which time several thousand grasshoppers have been carried at known temperatures from the time of hatching until they became adult. Differences in source of breeding stock and in the type of food used caused some variations in rate of development, but in computing the mean number of days in the nymphal stage at each constant temperature these differences have been disregarded and all available records have been included. Each rearing record in most cases includes from 5 to 10 adults reared from a single egg pod and all confined in a single rearing tube. Variations of several days in the length of the nymphal stage often occurred among individuals within a single group, and in such cases the number of days used for each rearing record is the weighted average of all the individuals included under that record. Based on all records available, the length of the nymphal stage and the percentage of total nymphal development per day were as follows:

	22°C.	27°C.	32°C.	37°C.
M. mexicanus	79.2 ± 1.05 days 1.26 ± .016 % dev.	41.9 ± .273 days 2.38 ± .017 % dev.	27.3 ± .207 days 3.66 ± .013 % dev.	23.1 ± .178 days 4.32 ± .037 % dev.
C. pellucida	No records " "	43.3 ± 1.22 days 2.29 ± .064 % dev.	25.0 ± .249 days 4.0 ± .04 % dev.	20.6 ± .436 days 4.85 ± .056 % dev.
M. femur-rubrum	65.2 ± .698 days 1.53 ± .016 % dev.	34.7 ± .583 days 2.88 ± .05 % dev.	30.8 ± .489 days 3.24 ± .053 % dev.	No records " "
M. packardi	No records " "	45.1 ± .332 days 2.21 ± .039 % dev.	27.5 ± 1.6 days 3.63 ± .212 % dev.	22.0 ± .556 days 4.58 ± .124 % dev.

The data on which this summary is based are given in Tables 16 and 17.

From the data presented it is evident that the rate of nymphal development for all four species used in the experiment increased directly with temperature from 22° to 37° C. Plotting percentage of development per day against tempera-

ture, curves are obtained which closely approximate the reciprocal growth curves figured by Sanderson and Peairs (16), and other workers. These are shown in Figure 6.

Table 16

Number of days and percentage of total development per day in the nymphal stage of M. mexicanus and C. pellucida at constant temperatures. From 5 to 10 specimens in each rearing record.

22°C.		27°C.		32°C.		37°C.	
Days in nymphal stage	Number of records	Days in nymphal stage	Number of records	Days in nymphal stage	Number of records	Days in nymphal stage	Number of records
			M. mexicanus				
72	2	34	2	19	1	17	1
74	1	35	1	21	7	18	3
76	3	37	2	22	13	19	3
78	1	38	9	23	7	20	5
79	2	39	4	24	1	21	8
80	1	40	13	25	12	22	10
82	1	41	9	26	26	23	15
85	1	42	8	27	10	24	7
86	1	43	3	28	15	25	8
94	1	44	2	29	10	26	3
		45	1	30	9	27	3
		46	1	31	9	30	1
		47	2	32	5	33	1
		48	2	33	7	35	1
		49	4	34	10	36	1
		50	2	35	7		
		51	2	36	2		
		54	1				
79.2±1.05	14	41.9±.273	68	27.3±.207	171	23.1±.178	70
			Percentage of total development per day				
1.26±.016		2.38±.017		3.66±.013		4.32±.037	
			C. pellucida				
		27	1	21	1	16	3
		38	2	22	6	17	2
		39	3	23	7	18	4
		40	2	24	5	19	4
		42	3	25	5	21	3
		44	2	26	3	22	1
		45	1	27	3	23	2
		47	1	30	1	24	3
		56	1	31	2	26	1
		58	1	32	1	27	1
		60	1	34	1	29	1
		43.3±1.22	18	25.0±.249	35	20.6±.436	25
			Percentage of total development per day				
		2.29±.064		4.00±.040		4.85±.056	

Table 17

Number of days and percentage of total development per day in the nymphal stage of M. femur-rubrum and M. packard at constant temperatures. From 5 to 10 specimens in each rearing record.

22°C.		27°C.		32°C.		37°C.	
Days in nymphal stage	Number of records	Days in nymphal stage	Number of records	Days in nymphal stage	Number of records	Days in nymphal stage	Number of records
			M. femur-rubrum				
59	1	30	1	26	2		
60	1	31	1	27	1		
61	3	32	1	28	3		
63	2	33	3	29	2		
64	1	34	2	31	2		
65	2	35	1	32	4		
67	1	36	1	34	3		
68	1	37	1	36	2		
69	1	38	1				
70	1	39	1				
71	1	41	1				
72	1						
65.2 ± .698	16	34.7 ± .533	14	30.8 ± .489	19		
Percentage of total development per day							
1.53 ± .016		2.88 ± .05		3.24 ± .053		5.0 ± .024	
			M. packardi				
		38	1	26	2	18	1
		41	1	27	3	19	1
		43	1	28	1	20	1
		45	2	29	3	21	2
		46	3	31	1	22	4
		49	1	34	1	23	1
		52	1			25	1
						29	1
		45.1 ± .832	10	27.5 ± 1.60	11	2.20 ± .556	12
Percentage of total development per day							
		2.21 ± .039		3.62 ± .212		4.54 ± .124	

These curves are decidedly different from the development curves for *M. mexicanus* eggs when kept at constant temperatures from the time they were laid (see Figure 7), the latter curves showing comparatively slow development at 22°, most rapid development at 27°, followed by a progressive slowing down of development at 32° and 37° C.

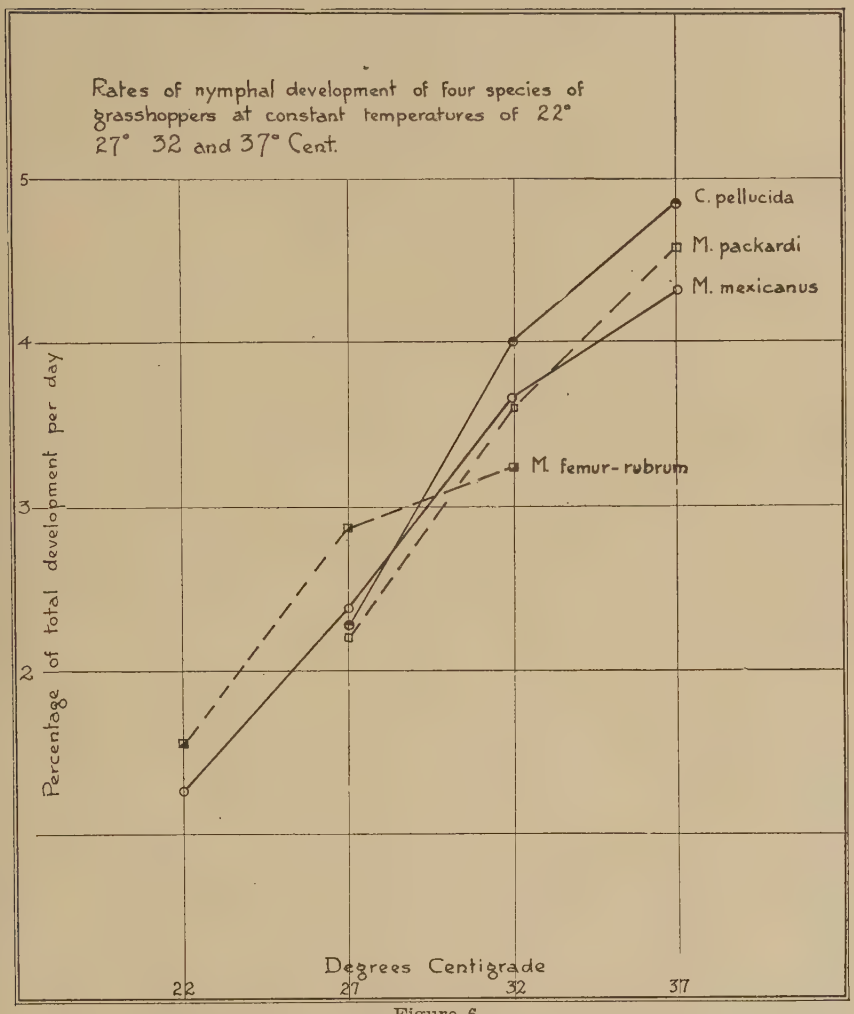

Figure 6

It is of interest to note that the curve for *Melanoplus femur-rubrum* shows a faster rate of development at 22° and 27° C. and a slower rate at 32° C. than any of the other three species. No records for this species at 37° C. were obtained because first instar nymphs never lived more than a few days at this temperature. This species is most commonly found in bushy areas along streams or in rank-growing grass, while the other three species prefer unshaded ground, sparsely covered with vegetation, and are thus adapted to a higher range of temperature.

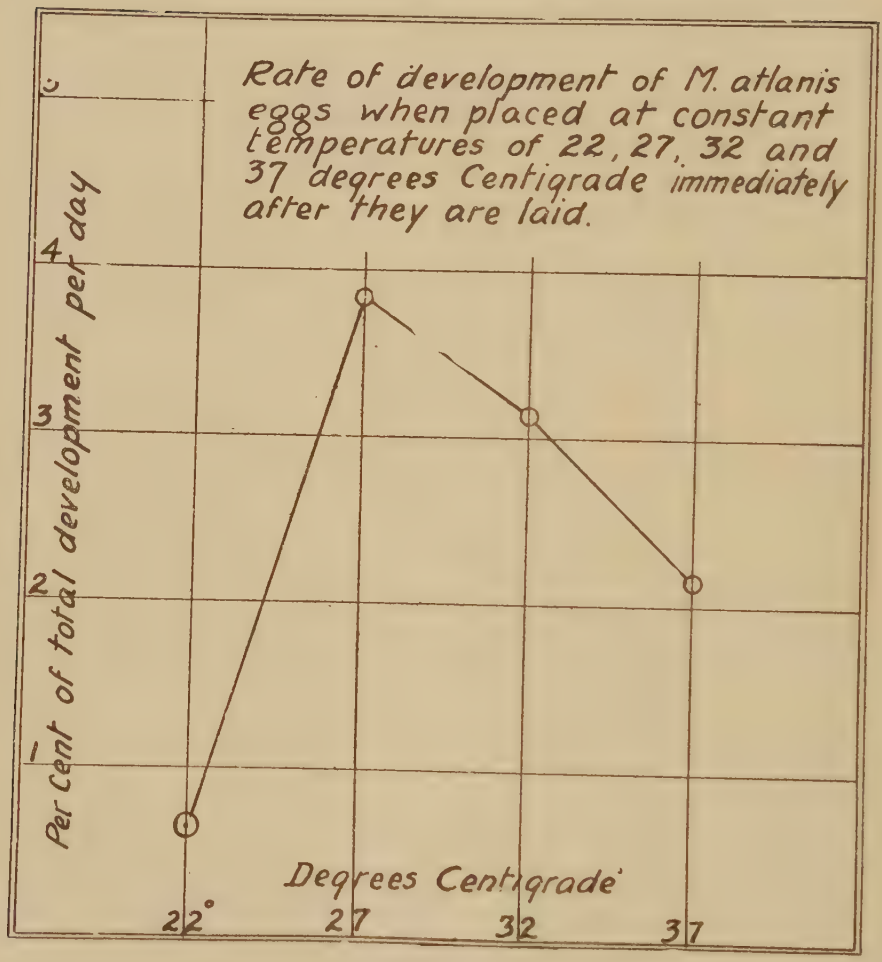

Figure 7

C. pellucida has a more restricted range of normal development than *M. mexicanus*, a fair percentage of nymphs of the latter reaching the adult stage at 22° C., while only one deformed adult of *C. pellucida* out of hundreds of nymphs started was ever obtained at this temperature.

The lack of rearing records of *Melanoplus packardi* at 22° C. is not significant since no attempt was made to rear them at that temperature.

Rate of Development at Constant and Alternating Temperatures

Experiments with nymphs of *M. mexicanus* held at constant and alternating temperatures from the time of hatching until they became adult, were conducted in much the same manner as the experiments with *M. mexicanus* and *C. pellucida* eggs described earlier in this paper (see page 25). Day-old nymphs from a large hatching of field-collected eggs from a single locality were divided into lots of 20 each. Four lots were held respectively at constant temperatures of 22°, 27°, 32°, and 37° C. for 24 hours each day; three lots were kept for 16 hours at 22° C., and at 27°, 32°, and 32° C. respectively for 8 hours daily; three lots were kept at 12° C. and at 27°, 32°, and 37° C. respectively for 8 hours daily. The rate of development under the three different sets of conditions was compared on the basis of the growth rate per day, or the percentage of total nymphal development accomplished in a 24-hour day. The results of these experiments are shown in Table 18. An explanation of the column headings and methods of obtaining "percentage of increase in rate of development" was given in connection with similar experiments with grasshopper eggs (see page 25), and will not be repeated.

Figure 8 is a graphic presentation of the data contained in Table 18. Percentages of total nymphal development per day were plotted against temperatures and the points connected by straight lines. The resulting curves are similar in appearance to curves showing the rate of development of overwintered eggs of *M. mexicanus* at constant and alternating temperatures. (See Figure 5, page 30.)

From an inspection of the table and the graph it is evident that nymphs of *M. mexicanus* kept for 16 hours each day at 22° C. and 8 hours at higher temperatures of 27°, 32°, and 37° C. developed faster than when held continuously at one constant temperature, the average acceleration for the three sets of temperatures being 12.4 per cent as compared with an average of 38.6 per cent in a similar experiment with *M. mexicanus* eggs at the same temperatures.

When nymphs were kept at 12° C. for 16 hours daily and 8 hours at higher temperatures of 27°, 32°, and 37° C., a still

TABLE 18.—Comparison of the rate of development of **M. mexicanus** nymphs at constant and alternating temperatures. Some nymphs held at constant temperatures from time of hatching until they became adult; others held at a low temperature for 16 hours daily and at higher temperatures for 8 hours daily. Twenty nymphs used for each set of temperatures

Constant temperatures			
Temp. ° C.	Days in nymphal stage	Percentage of total nymphal development per day	
22	85	1.176	
27	49	2.040	
32	30	3.333	
37	25	4.000	

Alternating temperatures											
16 hours daily at low temp. 8 hours daily at high temp.		Low temp.		High temp.		Total % dev. at const. temp. rate	Theoretical days in nymphal stage at const. temp.	Actual days in nymphal stage at altern. temp.	% dev. per day at const. temp.	% dev. per day at altern. temp.	% increase in rate of development at alternating temperature
		Days	% dev.	Days	% dev.						
22	27	40	46.8	20	40.8	87.6	68.5	60	1.46	1.66	13.7
22	32	32.66	38.21	16.33	54.37	92.5	52.9	49	1.89	2.04	7.9
22	37	27.33	31.97	13.66	54.64	86.6	47.3	41	2.11	2.44	15.6
										Average	12.4
12	27	71.33	0	35.66	72.74	72.74	147.	107	0.68	.93	36.7
12	32	40.66	0	20.33	67.69	67.79	90.	61	1.11	1.64	47.7
12	37	32.66	0	16.33	65.32	65.32	75.	49	1.33	2.04	53.3
										Average	45.8

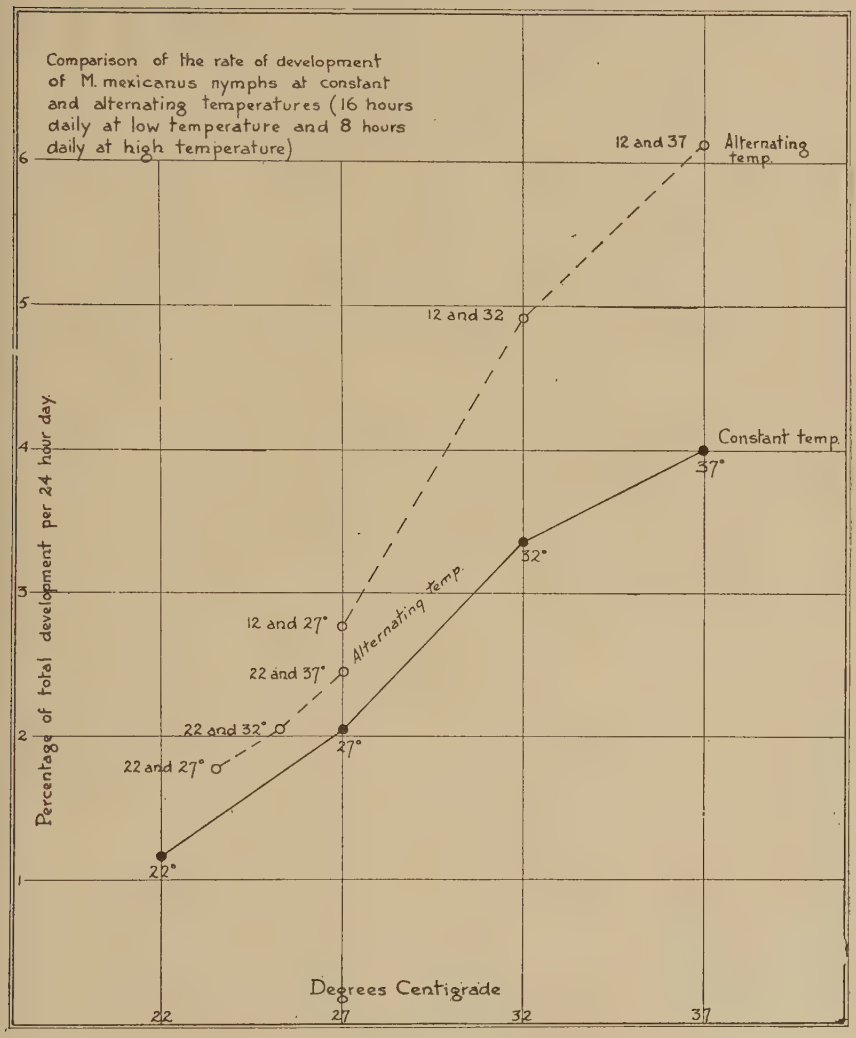

Figure 8

greater acceleration was obtained, the average for the three sets of temperatures being 45.8 per cent as compared with 56.5 per cent acceleration in the egg stage.

An experiment conducted primarily for the purpose of determining the relative amount of food consumed at constant and alternating temperatures, to be discussed later in this paper, also offers additional data on the growth rates at constant and

alternating temperatures. In this experiment day-old *M. mexicanus* nymphs were divided into lots of 10 each. Three lots were held continuously at constant temperatures of 27°, 32°, and 37° C. and three lots were held at 12° C. for 16 hours daily, and for 8 hours daily at higher temperatures of 27°, 32°, and 37° C., respectively. Their growth rates for the different combinations of temperature conditions are shown in Table 19. It will be noted that the results are quite similar to those obtained in the first experiment, the average accelerations in nymphs held for 16 hours at 12° C. and for 8 hours at higher temperatures being 38.0 per cent in the latter and 45.8 per cent in the former.

In computing accelerations in the experiment in which nymphs were held at 12° C. for 16 hours daily, it was assumed that no development took place at the low temperature. Nymphs at this temperature do not move unless disturbed, do not feed or molt, and die in from 10 to 14 days. It is very likely, however, that digestion and food assimilation go on at least for a short time after the nymphs enter the low temperature, and in view of this probability it must be admitted that the percentage of increase in rate of development as given above is slightly too high in those cases in which the nymphs were held at 12° C. Since no method of actually measuring the slight amount of development that might have taken place at 12° C. was known, the results are presented on the basis of zero development at that temperature.

In the experiments in which nymphs were held at a low temperature of 22° C. for 16 hours daily no such difficulty is encountered, for at this temperature the growth rate can be definitely measured. Since in every set of alternating temperatures used, the computed percentage of development at constant tmperature rate was always less than the actual amount of development obtained, it can be safely affirmed that alternations of temperatures result in pronounced acceleration in the growth rate of *M. mexicanus* nymphs.

In the discussion of grasshopper egg development at constant and alternating temperatures (see page 27) it was noted that holding eggs for 8 hours daily at 5° higher and for 16

TABLE 19.—Comparison of the rate of development of **M. mexicanus** nymphs at constant and alternating temperatures. Some nymphs held at constant temperatures from time of hatching until they became adult; others held at a low temperature for 16 hours daily and at higher temperatures for 8 hours daily. Ten nymphs used for each set of temperatures.

Constant temperatures

Temp. ° C.	Days in nymphal stage	Percentage of total nymphal development per day
27	54	1.98
32	27	3.70
37	24	4.16

Alternating temperatures

16 hours daily at low temp. 8 hours daily at high temp.		Low temp.		High temp.		Total % dev. at const. temp. rate	Theoretical days in nymphal stage at const. temp.	Actual days in nymphal stage at altern. temp.	% dev. per day at const. temp.	% dev. per day at altern. temp.	% increase in rate of development at alternating temperature
		Days	% dev.	Days	% dev.						
27	12	70	0	35	69.30	69.30	152	105	0.66	0.96	43.9
32	12	42	0	21	77.70	77.70	81	63	1.23	1.59	29.2
37	12	34	0	17	70.72	70.72	72	51	1.39	1.96	41.0
										Average	38.0

hours daily at 5° lower than any constant temperature or set of alternating temperatures, gave approximately the same amount of total development per day as holding them at the original temperature condition, and that in the one case where data were available the same relation held for a spread of 10 degrees. It now becomes of interest to ascertain whether a similar relation exists in the data on nymphal development at constant and alternating temperatures. This has been done by bringing together all the data in Table 18 between which the spread in temperature was either 5 or 10 degrees above the original temperature for 8 hours, and 5 or 10 degrees below it for 16 hours daily. Since *M. mexicanus* nymphs do not feed and are inactive below 17° C., the actual difference of 10° between 22° and 12° C. is considered as a difference of only 5 degrees in effective temperature.

Temperature ° C.	Days to hatch	Per cent development per day
22° Constant	85	1.17
12° and 27° Alternating	107	.93
Difference 5° C.	22	.24
27° Constant	49	2.04
22° and 32° Alternating	49	2.04
Difference 5° C.	0	0
27° Constant	49	2.04
12° and 37° Alternating	49	2.04
Difference 10° C.	0	0
22° and 27° Alternating	60	1.66
12° and 32° Alternating	61	1.64
Difference 5° C.	1	.02
22° and 32° Alternating	49	2.04
12° and 37° Alternating	49	2.04
Difference 5° C.	0	0

With the exception of the first set of temperatures the differences in growth rate are equal to or less than the differences in the rate for egg development at the same temperature conditions. This gives additional support to the principle suggested in connection with the discussion on egg development, which was stated as follows: "In any set of daily alternating temperatures within the range of normal development when the time spent at the low temperature is twice that at the high temperatures, the percentage of total development per day will

be equivalent to the percentage of development per day at a constant temperature equal to the mean of the two alternating temperatures." Applying this principle to the data on nymphal development shown in Table 18, it is found that 49 days were required for the combination of 16 hours at 22° C. and 8 hours at 32° C., and that exactly the same time was required at a constant temperature of 27° C., which is the mean of 22° and 32°. When nymphs were kept at 12° C. for 16 hours and at 37° for 8 hours daily, the time necessary to complete the stage was also 49 days. If the very slight amount of development below 17° C. is neglected, the mean effective temperature will again be 27° C. $\left[\frac{17+37}{2}\right]$

While the data on nymphal development, like those on egg development, are not extensive enough to warrant drawing definite conclusions, the relation between alternating and constant temperatures is so similar in both cases that it has seemed worth while to at least suggest the operation of a general principle.

TEMPERATURE LIMITS OF GENERAL ACTIVITY

The trained observer who studies grasshoppers can not fail to be impressed with the fact that they are great lovers of warmth and sunshine, and that their activities are very largely controlled by temperature. During cold weather they seek any shelter that offers a few degrees more of warmth than the open air, and so universal is this habit that a field which is literally swarming with grasshoppers at midday may not appear to contain a single grasshopper an hour after sundown if the evening is cool and shelter is available. As the morning sun warms the air and ground the grasshoppers slowly crawl from their hiding places, seek a position in the sun, and seem to fairly revel in the warmth of its rays. At such times they cluster thickly on stumps, boards, dry sod, dry dung, and the like, taking advantage of the fact that such materials are already several degrees warmer than the temperature of the air. As the temperature increases the grasshoppers start moving about and are active during the greater part of the day in

ordinary summer weather. If the day is extremely warm and the ground gets too hot for comfort, they choose their own temperature by crawling up on weeds or blades of grass, a distance of two inches above the ground offering a surprisingly wide range of temperature. Just before sundown they again seek objects which are warmer than the air and here arrange themselves in a position such that they will receive the greatest effect of the slanting rays of the setting sun. As the air continues to cool and the objects on which the grasshoppers are roosting give up their heat, they gradually crawl into clumps of grass, cracks in the soil, or other protected places. Should the evening be unusually warm no such reaction would occur, but instead the grasshoppers would remain active as long as temperature conditions were favorable.

These general facts are known to all workers who have studied grasshoppers under field conditions, but very few records can be found in the literature which state definitely at what temperatures the various activities take place. In the present study of *M. mexicanus* and *C. pellucida* many observations have been made of the temperatures at which these activities take place in nature and under controlled conditions in the laboratory.

TEMPERATURES AT WHICH ACTIVITIES TAKE PLACE UNDER FIELD CONDITIONS

Temperatures at "Beginning of Activity"

When grasshoppers which have become inactive because of low temperature are subjected to a gradually rising temperature, a point is eventually reached at which signs of activity are first noticed. Under field conditions, when this point is reached grasshoppers will be seen crawling out from their hiding places, moving slowly about in the open, seeking the warmest spots and arranging themselves broadside to the rays of the sun. This point will hereafter be designated as the "beginning of activity." Air and soil surface temperatures have been observed in many instances when the first signs of activity were noted. Air temperatures were taken by whirling a dry bulb mercury thermometer at 4 feet, and soil surface temperatures were taken by placing the bulb of the thermometer on the ground and covering it with a thin layer of soil.

Data showing the air and soil surface temperatures at which the "beginning of activity" occurs in nymphs and adults of *M. mexicanus* and *C. pellucida* under field conditions are given in Tables 20 to 23. The frequency distribution of these temperatures is shown in Figure 9.

TABLE 20.—Air and soil surface temperature at which "beginning of activity" was noted in nymphs of **M. mexicanus.**

Place	Date	Air temp.	Soil temp.	Place	Date	Air temp.	Soil temp.
Helena, Mont.	5/22/24	59° F.	72° F.	Willow Creek	6/16/24	58° F.	76° F.
Valier, Mont.	5/23/24	62	77	" "	6/17/24	60	78
Chester, Mont.	5/24/24	60	70	" "	6/20/24	61	80
Willow Creek	6/2/24	59	73	" "	6/21/24	62	76
" "	6/3/24	63	71	Havre, Mont.	5/16/26	61	75
" "	6/4/24	60	74	" "	5/24/26	63	72
" "	6/10/24	65	74	" "	5/25/26	62	74
" "	6/11/24	61	72	Wilsall, Mont.	6/6/27	59	73
" "	6/12/24	66	73	" "	6/7/27	62	79
" "	6/13/24	60	75	" "	6/8/27	60	80
" "	6/14/24	64	72	Average		61.3	74.6

TABLE 21.—Air and soil surface temperatures at which "beginning of activity" was noted in adults of **M. mexicanus.**

Place	Date	Air temp.	Soil temp.	Place	Date	Air temp.	Soil temp.
Willow Cr'k, Mont.	6/22/24	61° F.	90° F.	Willow Creek	7/17/24	65° F.	84° F.
" "	6/23/24	59	92	" "	7/19/24	60	79
" "	6/24/24	63	84	" "	7/21/24	62	76
" "	6/25/24	60	85	" "	7/22/24	58	80
" "	6/26/24	63	80	" "	7/24/24	56	87
" "	6/27/24	59	83	" "	7/25/24	60	77
" "	6/28/24	62	84	" "	7/26/24	66	76
" "	6/30/24	65	72	" "	7/29/24	61	77
" "	7/3/24	69	70	" "	7/30/24	63	78
" "	7/4/24	68	75	" "	7/31/24	61	73
" "	7/5/24	70	82	" "	8/1/24	63	74
" "	7/7/24	60	78	" "	8/2/24	61	71
" "	7/8/24	62	73	" "	8/4/24	58	81
" "	7/9/24	64	77	" "	8/5/24	62	75
" "	7/11/24	65	80	" "	8/6/24	56	73
" "	7/12/24	62	82	" "	8/7/24	60	71
" "	7/14/24	62	78	" "	8/8/24	57	82
" "	7/15/24	63	82	Wilsall, Mont.	8/23/25	60	75
" "	7/16/24	63	86	" "	8/24/25	61	79
				Average		61.8	78.9

In nymphs of *M. mexicanus* the lowest air temperature at which "beginning of activity" was noted was 59° F. (15° C.) and the highest 66° F. (18.9° C.), the average being 61.3° F. (16.3° C.). Fourteen out of a total of 21 observations ranged

TABLE 22.—Air and soil surface temperatures at which "beginning of activity" was noted in nymphs of **C. pellucida.**

Place	Date	Air temp.	Soil temp.	Place	Date	Air temp.	Soil temp.
Lakeview, Mont.	6/21/20	61° F.	72° F.	Minnie Lake, B. C.	6/4/25	49° F.	72° F.
" "	6/22/20	60	75	" "	6/5/25	58	73
" "	6/23/20	62	76	Merrit, "	6/6/25	59	68
" "	6/24/20	65	73	Bozeman, Mont.	6/18/25	64	77
" "	6/25/20	62	76	" "	6/19/25	61	79
Harney, Minn.	6/28/23	62	78	" "	6/20/25	62	76
" "	6/29/23	60	77	" "	6/21/25	61	76
" "	6/30/23	62	78	" "	6/24/26	60	78
" "	7/1/23	59	77	" "	6/25/26	61	75
" "	7/2/23	63	77		Average	60.6	75.9

TABLE 23.—Air and soil surface temperatures at which "beginning of activity" was noted in adults of **C. pellucida.**

Place	Date	Air temp.	Soil temp.	Place	Date	Air temp.	Soil temp.
Lakeview, Mont.	8/20/20	60° F.	70° F.	Bozeman, Mont.	7/20/25	61° F.	78° F.
" "	8/21/20	63	76	" "	7/21/25	62	82
" "	8/23/20	64	80	" "	7/23/25	62	79
" "	8/24/20	61	77	" "	7/24/25	63	77
" "	8/25/20	63	76	" "	7/25/25	59	78
Harney, Minn.	7/8/23	64	81	" "	8/3/25	63	74
" "	7/9/23	65	83	" "	8/4/25	64	73
" "	7/10/23	62	79	" "	7/14/26	62	76
" "	7/11/23	61	77	" "	7/15/26	63	80
" "	7/12/23	59	78	" "	8/6/26	60	79
" "	7/13/23	64	79	" "	8/7/26	64	75
" "	7/14/23	63	80	" "	8/11/26	58	76
					Average	62.0	77.6

from 60° to 63° F. (15.6° to 17.2° C.). The lowest soil surface temperature was 70° F. (21.1° C.) and the highest 80° F. (26.7° C.), the average being 74.6° F. (24.2° C.). Fifteen out of 21 observations ranged from 72° to 77° F. (22.2° to 25° C.).

In adults of the same species the lowest air temperature at which "beginning of activity" was noted was 56° F. (13.3° C.) and the highest 66° F. (18.9° C.), the average being 61.8° F. (16.6° C.). Twenty-three out of a total of 38 observations ranged from 60° to 63° F. (15.6° to 17.2° C.). The lowest soil temperature was 70° F. (21.1° C.) and the highest was 92° F. (33.3° C.), the average being 78.9° F. (26.1° C.). Nineteen out of a total of 38 observations ranged from 76° to 83° F. (24.4° to 28.3° C.).

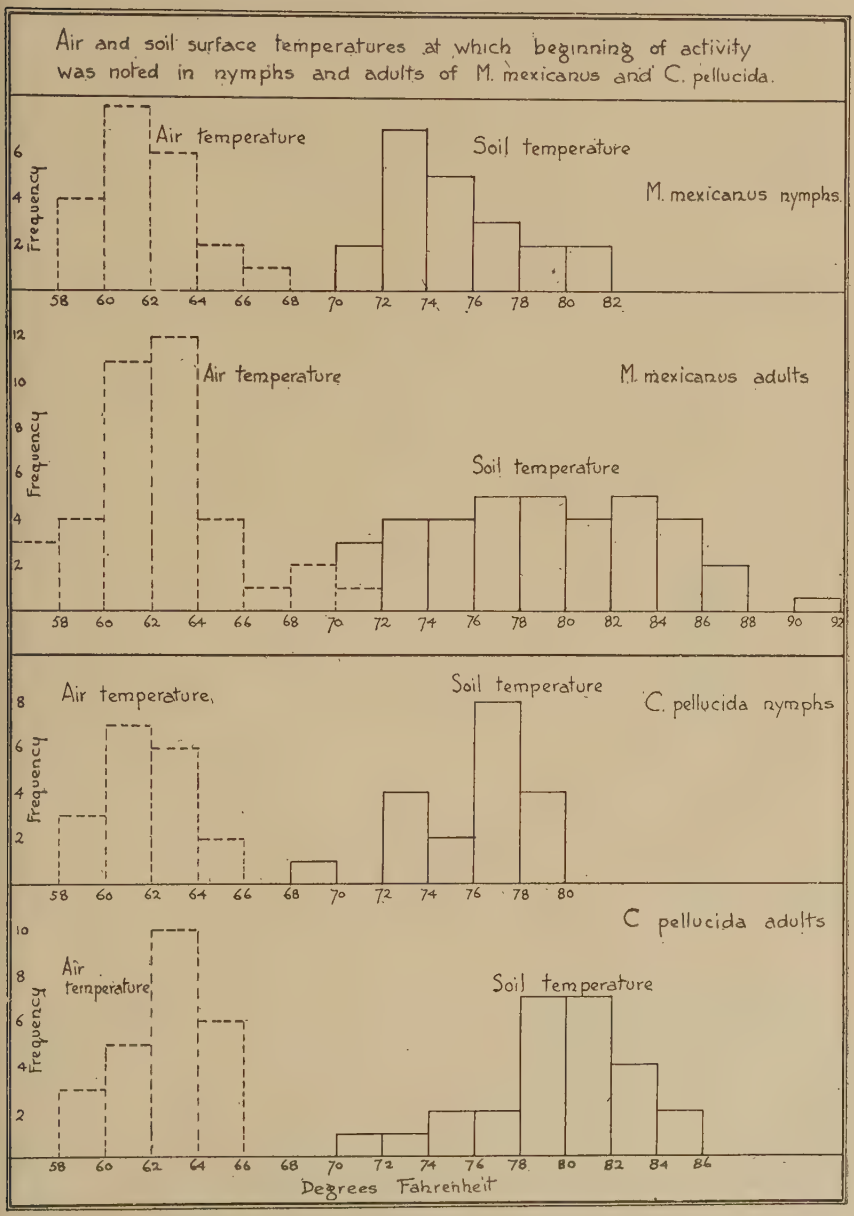
Air and soil surface temperatures at which beginning of activity was noted in nymphs and adults of M. mexicanus and C. pellucida.
Air temperature
Soil temperature
M. mexicanus nymphs
Frequency
M. mexicanus adults
C. pellucida nymphs
C pellucida adults
Degrees Fahrenheit

Figure 9

The wider range of temperature within which "beginning of activity" was noted in adults as compared with nymphs is undoubtedly due to the larger number of observations, 38 as compared with 21.

In nymphs of *C. pellucida* the lowest air temperature at which "beginning of activity" was noted was 49° F. (9.4° C.) and the highest 65° F. (18.3° C.), the average being 60° F. (15.6° C.). The observation of 49° F. (9.4° C.) made in British Columbia seems abnormal, but is explained by a corresponding soil temperature of 72° F. (22.2° C.). If this record is excluded the average is raised to 61° F. (16.1° C.) and the lowest temperature is 58° F. (14.4° C.), both of which correspond very closely to the temperatures recorded for nymphs of *M. mexicanus*. Thirteen out of a total of 19 observations range from 60° to 63° F. (15.6° to 17.2° C.). The lowest soil surface temperature was 72° F. (22.2° C.) and the highest 79° F. (26.1° C.), the average being 75.9° F. (24.3° C.). The peak of the frequency curve was from 76° to 77° F. (24.4° to 25° C.) which included 8 out of a total of 19 observations.

In adults of the same species the lowest air temperature at which "beginning of activity" was noted was 58° F. (14.4° C.) and the highest 65° F. (18.3° C.), the average being 62° F. (16.7° C.). Sixteen out of a total of 24 observations ranged from 62° to 63° F. (16.7° to 17.2° C.). The lowest soil surface temperature was 78° F. (21.1° C.) and the highest 82° F. (27.7° C.), the average being 77.6° F. (25.3° C.). Fourteen out of a total of 24 observations ranged from 78° to 81° F. (25.6° to 27.2° C.).

Temperatures at "Beginning of Normal Activity"

As already pointed out the daily activity of grasshoppers, following a cool night, begins with their crawling from shelter and seeking positions where they may secure the greatest effect of the sun. As the temperature continues to rise, a point is reached where they are no longer content to bask in the sunshine but instead begin to move about in search of food. This point is designated as the "beginning of normal activity."

Data showing the air and soil surface temperatures at which the "beginning of normal activity" occurs in nymphs and

adults of *M. mexicanus* and *C. pellucida* are given in Tables 24 to 27, and the frequency distribution of these temperatures is shown in Figure 10.

TABLE 24.—Air and soil surface temperatures at which "beginning of normal activity" was noted in nymphs of **M. mexicanus.**

Place	Date	Air temp.	Soil temp.	Place	Date	Air temp.	Soil temp.
Helena, Mont.	5/22/24	63° F.	91° F.	Willow Creek	6/16/24	61° F.	100° F.
Valier, Mont.	5/23/24	66	93	" "	6/17/24	65	94
Chester, Mont.	5/24/24	64	87	" "	6/20/24	67	92
Willow Creek, "	6/2/24	62	90	" "	6/21/24	64	90
" " "	6/3/24	66	88	Havre, Mont.	5/16/26	63	91
" " "	6/4/24	63	95	" "	5/25/26	65	90
" " "	6/10/24	68	84	Wilsall, Mont.	6/6/27	62	97
" " "	6/11/24	63	87	" "	6/7/27	64	91
" " "	6/12/24	68	82	" "	6/8/27	62	99
" " "	6/13/24	63	91	" "	6/9/27	62	102
" " "	6/14/24	66	93		Average	64.1	91.7

TABLE 25.—Air and soil surface temperatures at which "beginning of normal activity" was noted in adults of **M. mexicanus.**

Place	Date	Air temp.	Soil temp.	Place	Date	Air temp.	Soil temp.
Willow Cr'k, Mont.	6/22/24	65° F.	98° F.	Willow Cr'k, Mont.	7/17/24	70° F.	96° F.
" "	6/23/24	62	99	" "	7/19/24	63	100
" "	6/24/24	66	98	" "	7/21/24	66	97
" "	6/25/24	62	95	" "	7/22/24	65	95
" "	6/26/24	66	90	" "	7/24/24	59	97
" "	6/27/24	69	101	" "	7/25/24	65	94
" "	6/28/24	65	95	" "	7/26/24	70	93
" "	6/30/24	67	94	" "	7/28/24	68	92
" "	7/3/24	72	95	" "	7/29/24	65	93
" "	7/4/24	70	97	" "	7/30/24	65	88
" "	7/5/24	71	94	" "	7/31/24	65	88
" "	7/7/24	68	87	" "	8/1/24	67	84
" "	7/8/24	66	87	" "	8/2/24	65	82
" "	7/9/24	70	100	" "	8/4/24	60	96
" "	7/11/24	69	93	" "	8/5/24	60	95
" "	7/12/24	68	94	" "	8/6/24	60	93
" "	7/14/24	68	94	" "	8/7/24	69	89
" "	7/15/24	71	87	" "	8/8/24	63	93
" "	7/16/24	65	95		Average	66	93.6

In nymphs of *M. mexicanus* the lowest air temperature at which "beginning of normal activity" was noted was 61° F. (16° C.) and the highest 68° F. (20° C.), the average being 64.1° F. (17.9° C.). Fourteen out of a total of 21 observations ranged from 62° to 65° F. (16.7° to 18.3° C.). The lowest soil surface temperature noted was 82° F. (27.8° C.) and the highest 102° F. (38.9° C.), the average being 91.7° F. (33.2° C.).

TABLE 26.—Air and soil surface temperatures at which "beginning of normal activity" was noted in nymphs of **C. pellucida.**

Place	Date	Air temp.	Soil temp.	Place	Date	Air temp.	Soil temp.
Lakeview, Mont.	6/21/20	65° F.	93° F.	Minnie Lake, B. C.	6/4/25	56° F.	92° F.
" "	6/22/20	66	91	" "	6/4/25	65	90
" "	6/23/20	68	86	Merrit, B. C.	6/6/25	66	90
" "	6/24/20	69	90	Bozeman, Mont.	6/18/25	67	94
" "	6/25/20	66	101	" "	6/19/25	64	96
Harney, Minn.	6/28/23	67	98	" "	6/20/25	65	87
" "	6/29/23	65	100	" "	6/21/25	66	93
" "	6/30/23	64	97	" "	6/24/26	65	98
" "	7/1/23	62	98	" "	6/25/26	66	96
" "	7/2/23	66	88		Average	65.4	93.7

TABLE 27.—Air and soil surface temperatures at which "beginning of normal activity" was noted in adults of **C. pellucida.**

Place	Date	Air temp.	Soil temp.	Place	Date	Air temp.	Soil temp.
Lakeview, Mont.	8/20/20	66° F.	90° F.	Bozeman, Mont.	7/20/25	65° F.	93° F.
" "	8/21/20	68	80	" "	7/21/25	66	97
" "	8/23/20	67	85	" "	7/23/25	67	96
" "	8/24/20	68	86	" "	7/24/25	68	94
" "	8/25/20	67	88	" "	7/25/25	62	99
Harney, Minn.	7/8/23	69	96	" "	8/3/25	66	95
" "	7/9/23	68	103	" "	8/4/25	68	94
" "	7/10/23	65	98	" "	7/14/26	67	98
" "	7/11/23	64	99	" "	7/15/26	69	97
" "	7/12/23	62	101	" "	8/6/26	63	101
" "	7/13/23	70	97	" "	8/7/26	68	92
" "	7/14/23	71	96	" "	8/10/26	62	98
					Average	66.5	94.7

Twelve out of a total of 21 observations ranged from 90° to 95° F. (32.2° to 35° C.).

In adults of the same species the lowest air temperature at which "beginning of normal activity" was noted was 59° F. (15° C.) and the highest 72° F. (22.2° C.), the average being 66° F. (18.9° C.). Twenty-eight out of a total of 37 observations ranged from 64° to 71° F. (17.8° to 21.7° C.). The lowest soil surface temperature was 82° F. (27.8° C.) and the highest 101° F. (38.3° C.), the average being 93.6° F. (34.2° C.). Twenty-two out of a total of 37 observations ranged from 92° to 97° F. (33.3° to 36.1° C.).

In nymphs of *C. pellucida* the lowest air temperature at which "beginning of normal activity" was noted was 56° F. (13.3° C.) and the highest 69° F. (20.6° C.), the average being 65.4° F. (18.5° C.). Fifteen out of a total of 19 observations ranged from 64° to 67° F. (17.9° to 19.4° C.). The one record

of 56° F. (13.3° C.) is from British Columbia on the same date as the record of 49° F. (9.4° C.) for the "beginning of activity." Both are unusually low but, as already pointed out, are explained by high soil temperatures. The lowest soil surface temperature was 86° F. (30° C.) and the highest 101° F. (38.3° C.), the

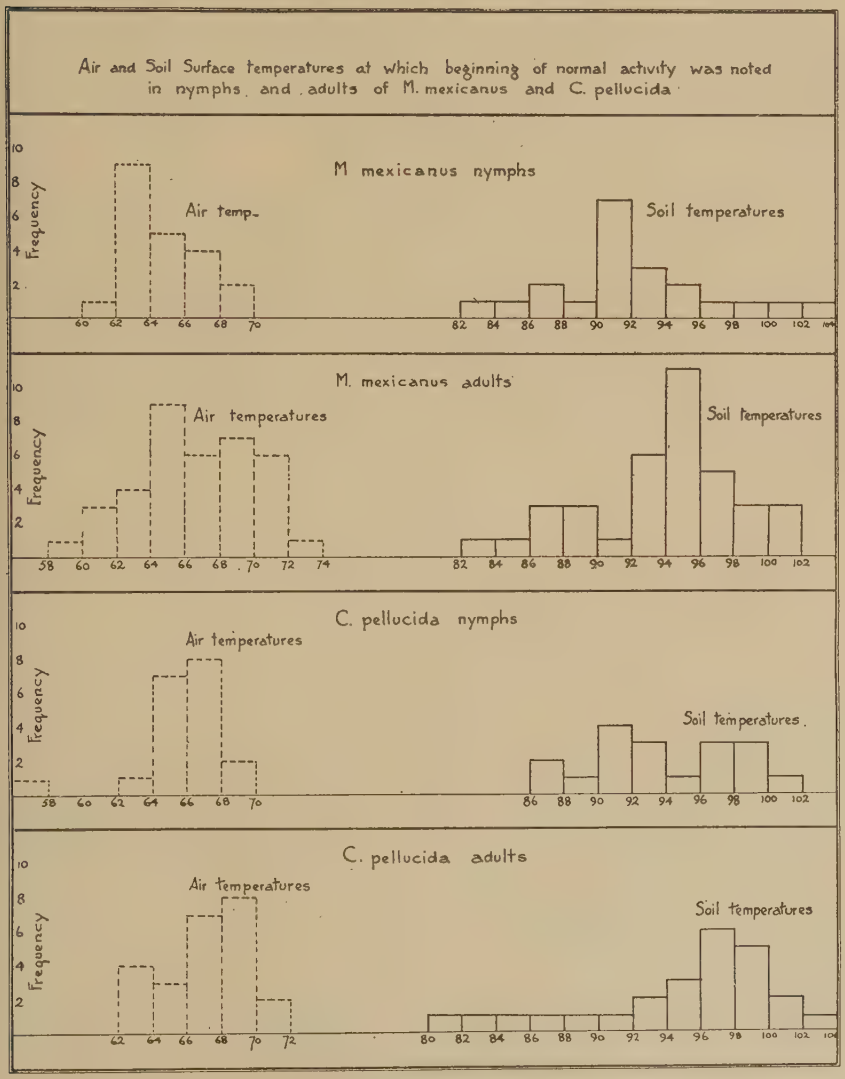

Figure 10

average being 93.7° F. (34.3° C.). Fourteen out of a total of 19 observations ranged from 90° to 99° F. (32.2° to 37.2° C.).

In adults of the same species the lowest air temperature at which "beginning of normal activity" was noted was 62° F. (16.7° C.) and the highest 71° F. (21.7° C.), the average being 66.5° F. (19.2° C.). Fifteen out of a total of 24 observations ranged from 66° to 69° F. (18.9° to 20.6° C.). The lowest soil surface temperature was 80° F. (26.7° C.) and the highest 103° F. (39.4° C.), the average being 94.7° F. (34.8° C.). Fourteen out of 24 observations ranged from 94° to 99° F. (34.4° to 37.2° C.).

Temperatures at Which Various Normal Activities Take Place

Within the range of "normal activity," which has been shown to begin at air temperature of approximately 65° F. (18.3° C.) and soil surface temperature of about 90° F. (32.2° C.), are included such special activities as migrations of nymphs, flight of adults, egg laying and feeding. These in turn have rather definite temperature limits, which will be discussed in some detail.

Temperatures at Which Migrations of Nymphs Take Place

Nymphs of both *M. mexicanus* and *C. pellucida* are migratory in habit, the movement of migratory bands being to a large extent controlled by temperature.

Twelve observations made when bands of *M. mexicanus* were beginning to migrate gave average air and soil surface temperatures of 71.1° and 93.8° F. (21.7° and 34.3° C.) respectively. A similar number of observations made just as migrations stopped gave average air and soil surface temperatures of 70.6° and 92.8° F. (21.5° and 33.8° C.), indicating that migrations start and stop at practically the same temperatures.

Eight observations made when bands of *C. pellucida* were beginning to migrate gave average air and soil surface temperatures of 67.1° and 92.8° F. (19.5° and 33.8° C.) respectively. A similar number of observations made just as migrations stopped gave average air and soil surface temperatures of 66.1° and 86.7° F. (18.9° and 30.3° C.) which are also very close to the temperatures at the start of migration.

It was observed several times that migrating would alternately start and stop as passing clouds exposed or obscured the sun. This was at first thought to be a light reaction, but when air and soil surface temperatures were taken it seemed explainable as a temperature reaction. An example of this was seen at Minnie Lake, B. C., on June 5, 1925. A large swarm of migrating *C. pellucida* nymphs was observed as follows:

Time	Weather condition	Degree of activity	Air temp.	Soil surface temp.
2:40	Bright	Full migration	65° F.	82° F.
2:45	Clouded	Migration stopped	56	60
2:50	Bright	Migration starting	62	80
3:00	Clouded	Migration slowing	60	75
3:05	Bright	Full migration	66	83
3:15	Clouded	Migration stopped	55	60

Similar data on nymphs of *M. mexicanus* were obtained by R. L. Shotwell, of the Bureau of Entomology, who made observations on a migrating band of nymphs at Havre, Montana, on June 9, 1925. I am indebted to him for the following data:

Time	Weather condition	Degree of activity	Air temp.	Soil surface temp.
10:00	Bright	Migration first noticed	68.0° F.	93.0° F.
11:10	Cloudy	Migration stopped	65.3	87.8
11:15	Bright	Slight movement	66.2	87.8
11:15	Bright	Migration increases	68.0	87.8
11:20	Cloudy	Migration almost stopped	66.2	87.8
11:25	Bright	Migration increases	68.2	89.6
11:28	Bright	Full migration	71.6	93.2
11:32	Cloudy	Migration slowing	68.0	93.2
11:40	Bright	Full migration	71.6	104.0

It is interesting to note that Sviridenko (18), working in Russia, makes the following statement: "Larval swarms of *Dociostaurus maroccanus* Thnbg. start their daily march in the morning when the temperature reaches about 23°-27° C. (73.4°-80.6° F.) and they stop whenever it drops to the same level, whether in the evening or during the day owing to clouds or wind."

Data from which were obtained the average air and soil temperatures at the beginning and ending of migration are given in Table 28.

TABLE 28.—Air and soil surface temperatures at which the beginning and ending of migration was noted in nymphal bands of M. mexicanus and C. pellucida.

Place	Date	Migration begins		Migration ends	
		Air temp.	Soil temp.	Air temp.	Soil temp.
			M. mexicanus		
Willow Creek, Mont.	6/3/24	70° F.	95° F.	71° F.	93° F.
" "	6/10/24	72	92	73	94
" "	6/12/24	69	95	72	90
" "	6/17/24	68	90	70	92
" "	6/20/24	73	100	72	95
" "	6/24/24	66	95	65	93
" "	6/25/24	66	99	62	97
" "	6/25/24	75	99	73	92
Havre, Mont.	6/3/26	73	85	74	90
" "	6/7/26	....	....	76	90
" "	6/8/26	82	90	....	....
" "	6/9/26	68	93	68	95
" "	6/9/26	72	93	68	93
Average		71.1	93.8	70.6	92.8
			C. pellucida		
Lakeview, Mont.	6/21/20	69	98	70	96
" "	6/22/20	71	101	72	95
" "	6/23/20	74	92	72	95
" "	6/24/20	70	97	70	96
Minnie Lake, B. C.	6/4/25	60	90	60	78
" "	6/4/25	65	90	60	76
" "	6/5/25	62	80	60	78
Merrit, B. C.	6/6/25	66	95	65	80
Average		67.1	92.8	66.1	86.7

Temperatures at Which Flights of Adults Take Place

When *M. mexicanus* or *C. pellucida* is present in large numbers distinct flights often occur. These take place at fairly high temperatures. Twelve observations made at the beginning of flights of *M. mexicanus* gave average air and soil surface temperatures of 84.1° F. (28.9° C.) and 112° F. (44.4° C.) respectively. No flights were observed at air temperature lower than 75° F. (23.9° C.) or soil surface temperature lower than 95° F. (35° C.). Ten observations made at the beginning of flight of *C. pellucida* gave average air and soil surface temperatures of 75° F. (23.9° C.) and 102° F. (38.9° C.) respectively. In this species no flights were observed at air temperature lower than 73° F. (22.8° C.), or soil surface temperature lower than 90° F. (32.2° C.). Data on which these statements are based are found in Table 29.

TABLE 29.—Air and soil surface temperatures at which "beginning of flying" was noted in **M. mexicanus** and **C. pellucida.**

M. mexicanus				C. pellucida			
Place	Date	Air temp.	Soil temp.	Place	Date	Air temp.	Soil temp.
Willow Cr'k, Mont.	7/2/24	90° F.	134° F.	Lakeview, Mont.	8/20/20	76° F.	100° F.
" "	7/3/24	90	116	" "	8/21/20	75	90
" "	7/8/24	75	95	" "	8/21/20	76	95
" "	7/8/24	76	95	" "	8/23/20	76	105
" "	7/9/24	88	119	" "	8/23/20	78	108
" "	7/10/24	86	95	" "	8/24/20	74	95
" "	7/10/24	85	97	" "	8/24/20	73	92
" "	7/11/24	81	122	" "	8/24/20	75	95
" "	7/12/24	80	102	Harney, Minn.	8/29/23	77	112
" "	7/14/24	86	127	" "	8/29/23	75	110
" "	7/14/24	91	127				
" "	7/15/24	82	115				
Average		84.1	112			75.5	102

Flights do not depend upon high temperature alone but are greatly influenced by wind. Flights are seldom seen during a strong wind or when the air is very still. A light breeze combined with high temperature offers optimum conditions for flight.

Rockwood (15) records flights of grasshoppers at night when the air temperature was approximately 80° F. (26.7° C.), and draws attention to records of other workers which indicate that this habit is not uncommon during unusually warm weather.

Temperatures at Which Egg Laying Takes Place

Egg laying in both *M. mexicanus* and *C. pellucida* is very definitely controlled by temperature. In *M. mexicanus* egg laying has never been observed at air temperature below 69° F. (20.6° C.) or soil surface temperature below 98° F. (36.7° C.). Twelve observations made when the first egg laying of the day was noted gave an average air temperature of 71.1° F. (21.8° C.) and soil surface temperature of 99.8° F. (37.7° C.).

In *C. pellucida* ten observations give slightly higher averages, the air temperature being 72.4° F. (22.4° C.) and the soil surface temperature 101.3° F. (38.5° C.). Data on which these statements are made are given in Table 30.

Egg laying in both species continues at higher temperatures until the grasshoppers are forced to climb vegetation to escape heat which, as will be shown, is at air temperatures of about 80° F. (26.7° C.) and soil surface temperatures of approxi-

TABLE 30.—Air and soil surface temperatures at which "beginning of egg laying" was noted in **M. mexicanus** and **C. pellucida.**

M. mexicanus				C. pellucida			
Place	Date	Air temp.	Soil temp.	Place	Date	Air temp.	Soil temp.
Willow Cr'k, Mont.	7/9/24	70° F.	100° F.	Lakeview, Mont.	8/20/20	72° F.	102° F.
" "	7/10/24	71	99	" "	8/21/20	73	99
" "	7/11/24	70	101	" "	8/23/20	72	98
" "	7/14/24	72	98	" "	8/24/20	71	99
" "	7/15/24	71	98	Harney, Minn.	7/29/23	72	104
" "	7/17/24	70	102	" "	7/30/23	72	105
" "	7/24/24	72	102	Bozeman, Mont.	7/20/25	74	98
" "	7/25/24	71	104	" "	7/24/25	73	102
" "	7/28/24	72	98	" "	8/3/25	72	104
" "	7/29/24	73	100	" "	8/4/25	73	102
" "	7/30/24	73	98				
Wilsall, Mont.	8/23/25	69	98				
Average		71.1	99.8			72.4	101.3

mately 107° to 113° F. (41.7° to 45° C.). However, egg laying often continues at higher air temperatures, the females at such times seeking cooler ground in the shade of plants, stones, and other objects.

While no definite series of observations has been made to determine at what point egg laying stops when the temperature is falling, it has been observed in a general way to be very close to the same point at which egg laying begins.

Temperatures at Which Feeding on Vegetation Takes Place

Definite temperatures at which various degrees of feeding on vegetation take place are difficult to obtain since more or less feeding goes on throughout the entire range of activity. Occasional nibbling at grass may be seen as soon as the grasshoppers start moving in the morning and it continues even while they are clustered in the warmer areas in the late afternoon. Maximum feeding in both nymphs and adults begins at the temperature already given for the "beginning of normal activity." It continues for several hours and then gradually tapers off as the desire for food becomes less keen. Maximum feeding is interrupted when air temperatures go much above 80° F. (26.7° C.), or soil surface temperatures above 113° F. (45° C.), the grasshoppers then climbing vegetation where most of them remain motionless, only now and then nibbling on the vegetation upon which they are resting.

Temperatures at Which Feeding on Poisoned Bran Mash Takes Place

In connection with experiments conducted to determine the most attractive poisoned bran mash bait for grasshoppers, an excellent opportunity was afforded to also determine the range of temperature at which feeding on these baits took place. Bait experiments with *C. pellucida* were conducted at Harney, Minnesota, for 11 days during the summer of 1923. In 1924 similar experiments with *M. mexicanus* were conducted at Willow Creek, Montana, for 35 days. At 10-minute intervals counts were made of the grasshoppers actually feeding at the various baits. In the Minnesota experiments the total number of grasshoppers counted was 15,659, and in the Montana experiments 62,210. Air temperatures and relative humidity were recorded by a hygro-thermograph at 4 feet above the ground. In the Montana experiments soil surface temperature readings were made at 10-minute intervals.

In studying the relation of temperature to the number of grasshoppers feeding, hourly records for each bait were added to obtain the total number feeding for each hour of the day. Mean hourly temperatures were computed by taking one-half the sum of the temperatures at the beginning and the end of each hour. Comparisons of the amount of feeding during different hours were made on a basis of hourly percentages of the total number of grasshoppers feeding per day. For example, if a total of 400 grasshoppers fed during one day and 200 of them fed during the hour between 10 and 11 a. m. the percentage of feeding for that hour would be 50. Hourly records for 27 typical days in Montana and 9 in Minnesota are shown graphically in Figures 11 to 14.

An examination of the graphs shows that *M. mexicanus* under Montana conditions feeds sparingly at bran mash baits at air temperatures of 55° to 63° F. (12.7° to 17.2° C.) and soil surface temperatures of 70° to 94° F. (21° to 34.4° C.), more actively at air temperatures of 64° to 67° F. (17.7° to 19.4° C.) and soil surface temperatures of 95° to 103° F. (35° to 39.4° C.), and most actively at air temperatures of 68° to 78° F. (20° to 25.5° C.) and soil surface temperatures of 104° to 112° F. (40° to 44.4° C.).

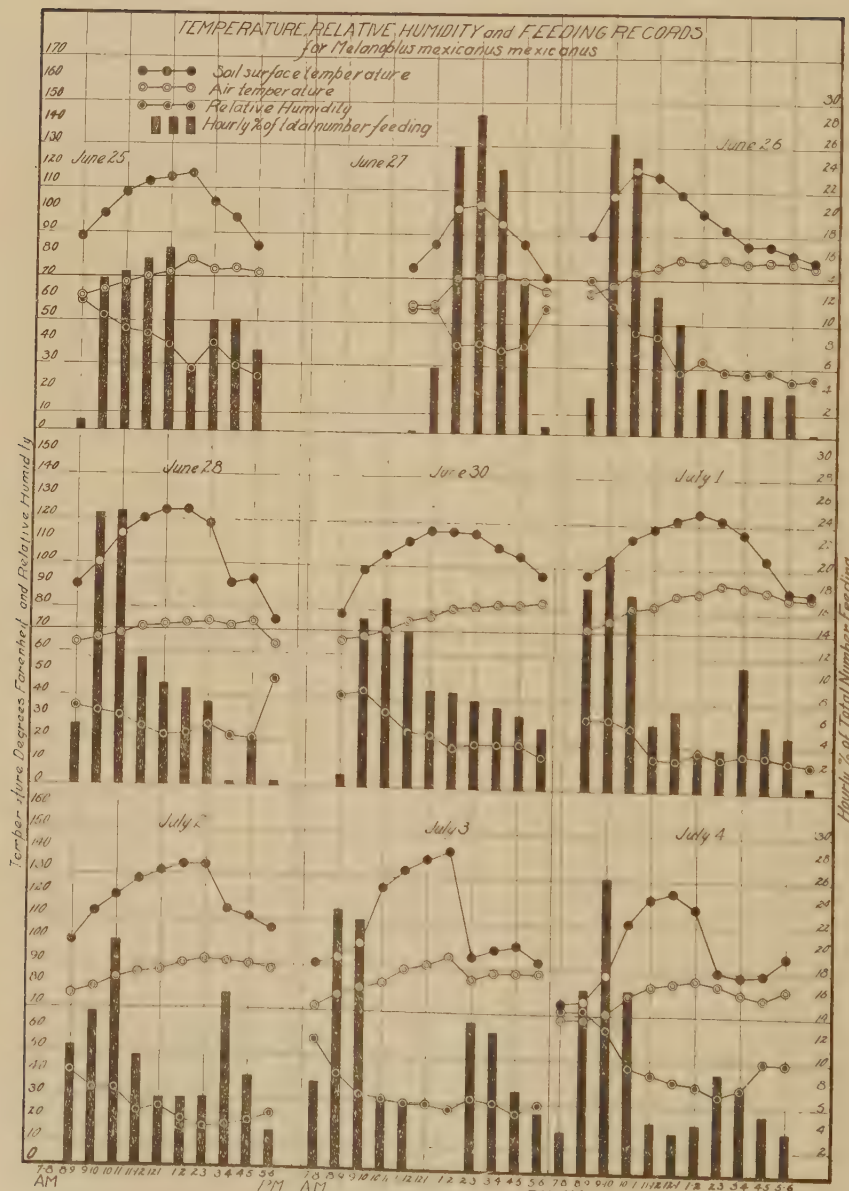
TEMPERATURE, RELATIVE HUMIDITY and FEEDING RECORDS
for Melanoplus mexicanus mexicanus
Soil surface temperature
Air temperature
Relative Humidity
Hourly % of total number feeding
June 25
June 27
June 26
June 28
June 30
July 1
July 2
July 3
July 4
Temperature Degrees Fahrenheit and Relative Humidity
Hourly % of Total Number Feeding
AM
PM

Figure 11

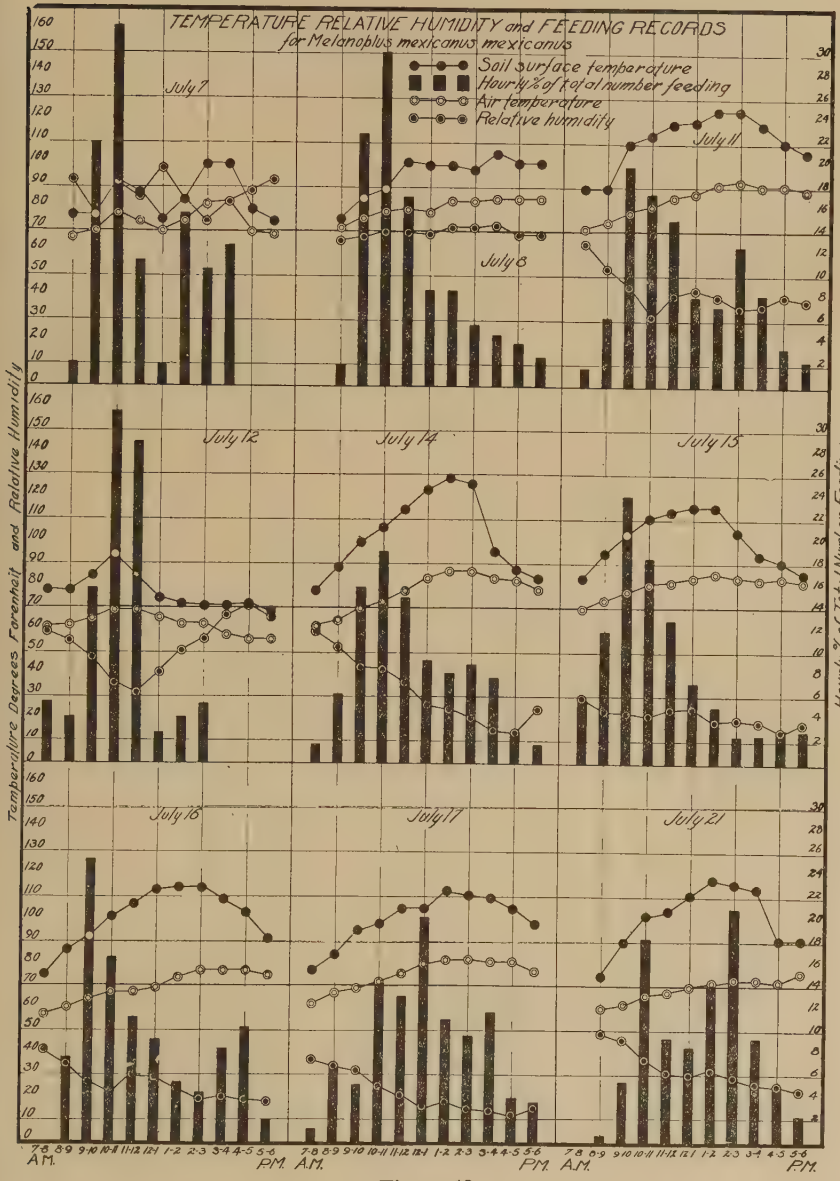
TEMPERATURE RELATIVE HUMIDITY and FEEDING RECORDS
for Melanoplus mexicanus mexicanus
Soil surface temperature
Hourly % of total number feeding
Air temperature
Relative humidity
July 7
July 8
July 11
July 12
July 14
July 15
July 16
July 17
July 21
Temperature Degrees Farenheit and Relative Humidity
Hourly % of Total Number Feeding
A.M.
P.M.

Figure 12

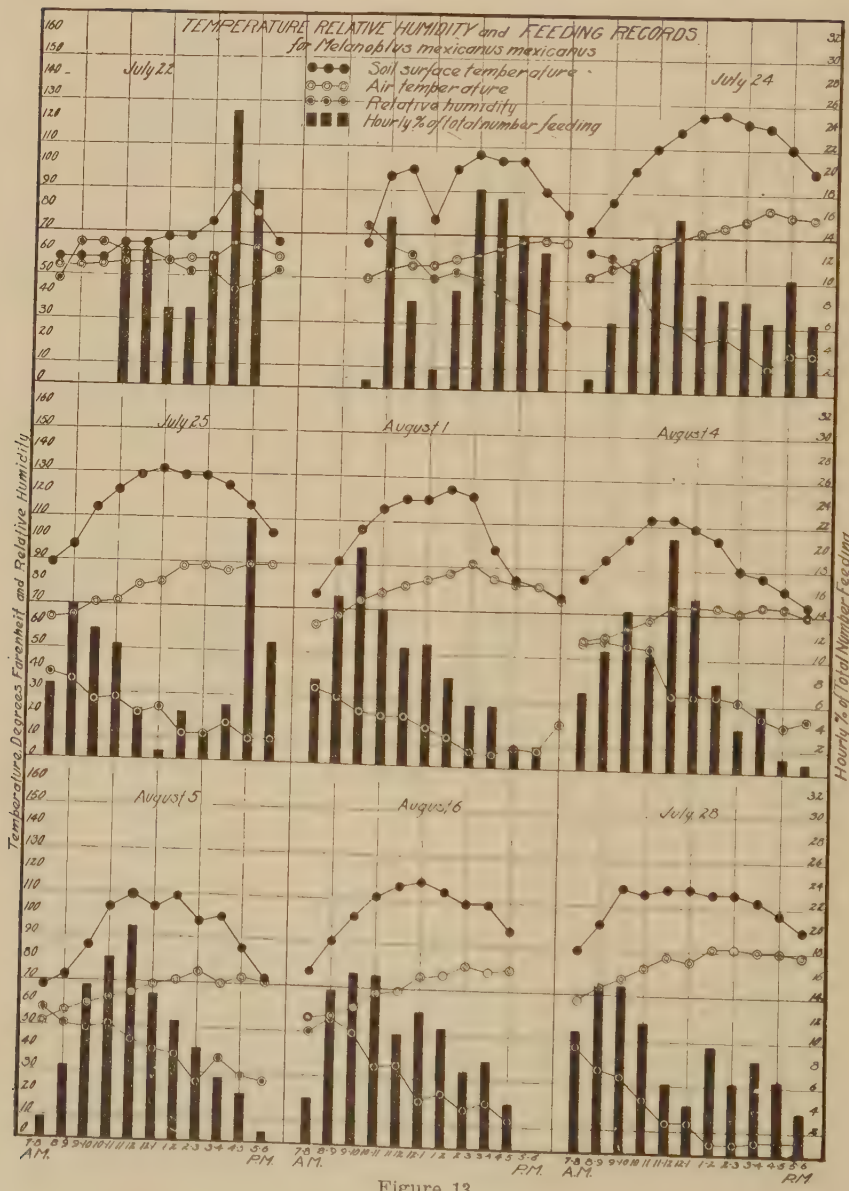
TEMPERATURE RELATIVE HUMIDITY and FEEDING RECORDS
for Melanoplus mexicanus mexicanus
Soil surface temperature
Air temperature
Relative humidity
Hourly % of total number feeding
July 22
July 24
July 25
August 1
August 4
August 5
August 6
July 28
Temperature, Degrees Farenheit and Relative Humidity
Hourly % of Total Number Feeding
A.M.
P.M.

Figure 13

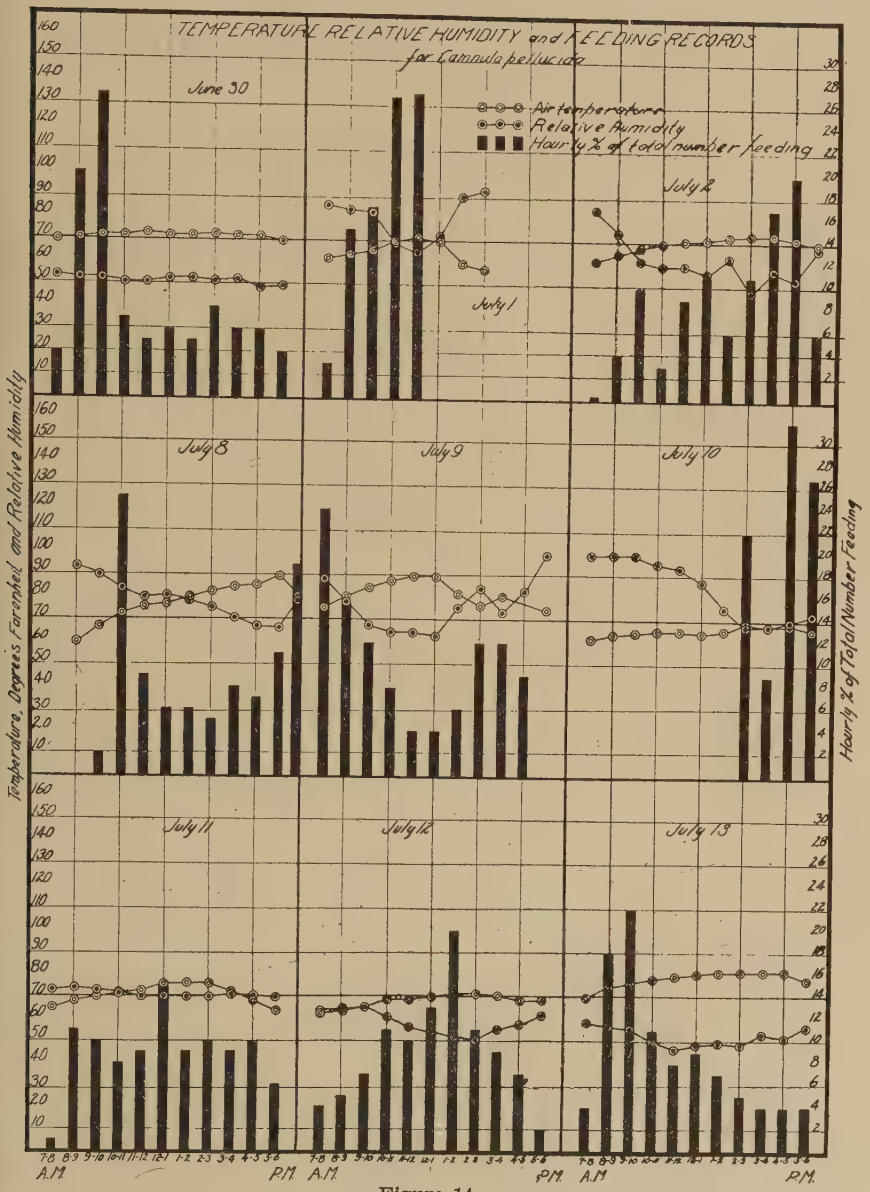
TEMPERATURE RELATIVE HUMIDITY and FEEDING RECORDS
for Camnula pellucida
Air temperature
Relative humidity
Hourly % of total number feeding
June 30
July 1
July 2
July 8
July 9
July 10
July 11
July 12
July 13
Temperature, Degrees Farenheit and Relative Humidity
Hourly % of Total Number Feeding
A.M.
P.M.

Figure 14

In 20 out of the 27 daily records shown in the graphs, the hour of maximum feeding for the day took place at air temperatures ranging from 68° to 78° F. (20° to 25.5° C.). As a general rule feeding decreased very rapidly whenever the air temperature went above 80° F. (26.7° C.) or the soil surface temperature went above 113° F. (45° C.). When such periods of high temperature are terminated by rather sudden drops in temperature, quite active feeding at poisoned bran mash sometimes takes place at air temperatures which are somewhat above the optimum for general feeding. Such secondary peaks may be noted in the graphs containing records for July 1 to 3 and July 25.

C. pellucida under Minnesota conditions has a somewhat narrower range of temperature at which feeding takes place. The graphs show that it feeds sparingly at bran mash baits at air temperatures of 62° to 66° F. (16.6° to 18.9° C.), more actively at air temperatures of 67° to 70° F. (19.4° to 21.1° C.), and most actively at air temperatures from 71° to 77° F. (21.6° to 25° C.). During 8 of the 9 days shown in the graphs, the hour of maximum feeding occurred at air temperatures ranging from 72° F. (22.2° C.) to 77° F. (25° C.). On days when hourly mean temperatures are below this range the time of heaviest feeding occurs during the hour when the highest temperature for the day is first reached. Feeding decreases very rapidly at air temperatures above 80° F. (26.6° C.).

Temperatures at the Beginning of "Climbing to Escape Heat"

If, after normal activity has begun, the air and soil surface temperatures continue to rise, a point is reached at which grasshoppers will leave the unshaded ground and seek more desirable temperatures by climbing weeds and blades of grass. The temperature at the surface of the ground at such time is, of course, much higher than that of the air slightly above it. The wide range of temperature from which the grasshopper can choose by merely moving 2 inches up or down a blade of grass is shown in comparative temperatures noted at Harney, Minnesota, on July 9, 1923.

From these temperatures it is seen that when the air temperature was 90° F. the ground surface temperature was 134.6°

Time	Temperature of ground surface	Temperature 2 in. above ground	Temp of air at 4 ft.
11:30 a. m.	134.6° F. (57° C.)	96.8° F. (36° C.)	90° F. (32.2° C.)
12:30 p. m.	139.0° F. (59.5° C.)	100.4° F. (38° C.)	92° F. (33.3° C.)
1:30 p. m.	105.8° F. (41.0° C.)	89.6° F. (32° C.)	85° F. (29.4° C.)
2:30 p. m.	96.8° F. (36.0° C.)	86.0° F. (30° C.)	77° F. (25.0° C.)

F. and that a grasshopper could have reached a position 39.8° F. cooler by climbing to a position 2 inches above the ground, where the air temperature registered 96.8° F.

Air and soil surface temperatures noted at the "beginning of climbing to escape heat" are shown in Table 31.

TABLE 31.—Air and soil surface temperatures at which beginning of "climbing to escape heat" was noted in adults of **M. mexicanus** and **C. pellucida.**

M. mexicanus				C. pellucida			
Place	Date	Air temp.	Soil temp.	Place	Date	Air temp.	Soil temp.
Willow Cr'k, Mont.	6/21/24	78° F.	109° F.	Lakeview, Mont.	8/23/20	78° F.	105° F.
" "	6/25/24	76	112	" "	8/24/20	79	105
" "	6/20/24	75	113	Harney, Minn.	7/8/23	85	108
" "	6/28/24	72	116	" "	7/9/23	85	107
" "	6/30/24	78	115	" "	7/11/23	76	110
" "	7/1/24	82	113	" "	7/13/23	82	109
" "	7/2/24	83	115	Bozeman, Mont.	7/20/25	79	108
" "	7/3/24	84	114	" "	7/24/25	81	107
" "	7/4/24	86	110	" "	8/3/25	78	109
" "	7/10/24	81	106	" "	8/4/25	80	100
" "	7/11/24	87	115				
" "	7/14/24	78	112				
" "	7/15/24	84	113				
" "	7/17/24	82	113				
" "	7/28/24	86	114				
" "	8/1/24	76	112				
	Average	80.5	112.6		Average	80.3	107.4

The lowest air temperature at which "beginning of climbing to escape heat" was noticed in adults of *M. mexicanus* was 72° F. (22.2° C.) and the highest 87° F. (30.6° C.), the average being 80.5° F. (26.9° C.). There is no decided peak to the frequency distribution curve. The lowest soil surface temperature at which this reaction was noted was 106° F. (41.1° C.) and the highest 116° F. (46.7° C.), the average being 112.6° F. (44.8° C.). Twelve out of a total of 16 observations ranged from 112° to 115° F. (44.4° to 46.1° C.).

The lowest air temperature at which "beginning of climbing to escape heat" was noted in adults of *C. pellucida* was 76° F. (24.4° C.) and the highest 85° F. (29.4° C.), the average

being 80.3° F. (26.8° C.). The lowest soil surface temperature was 104° F. (40° C.) and the highest 111° F. (43.9° C.), the average being 107.4° F. (41.9° C.).

The narrower range and the more pronounced peak in the frequency distribution curves of the soil surface temperatures as compared with the air temperature indicate that "climbing to escape heat" is much more dependent upon the former than the latter.

Temperatures at "Beginning of Clustering" Preparatory to Inactivity

If a falling temperature occurs during normal grasshopper activity a point is eventually reached at which normal activities cease and the grasshoppers start gathering in the warmest locations and arranging themselves in such positions as will give them the greatest benefit from the sun's rays. When grasshoppers are numerous this often results in their gathering together in masses or clusters, and for want of a better term this reaction is referred to as the "beginning of clustering."

Air and soil surface temperatures noted at the "beginning of clustering" are given in Tables 32 and 33, and their frequency distribution is shown in Figure 15.

In nymphs of *M. mexicanus* the lowest air temperature at which "beginning of clustering" was noted was 65° F. (18.3° C.) and the highest 74° F. (23.3° C.), the average being 68.9° F. (20.5° C.). Nine out of a total of 12 observations ranged from 66° to 71° F. (18.9° to 21.7° C.). The lowest soil surface temperature was 82° F. (27.8° C.) and the highest 90° F. (32.3° C.), the average being 86.6° F. (30.3° C.). Nine out of a total of 12 observations ranged from 84° to 89° F. (28.9° to 31.7° C.).

In adults of the same species the lowest air temperature at which this reaction took place was 65° F. (18.3° C.) and the highest 74° F. (23.3° C.), the average being 71° F. (21.7° C.). Twelve out of a total of 15 observations ranged from 70° to 73° F. (21.1° to 22.8° C.). The lowest soil surface temperature was 74° F. (23.3° C.) and the highest 96° F. (35.6° C.), the average being 88.4° F. (31.3° C.). Ten out of a total of 15 observations ranged from 88° to 93° F. (31.1° to 33.9° C.).

In nymphs of *C. pellucida* the lowest air temperature at which "beginning of clustering" was noted was 64° F. (17.8°

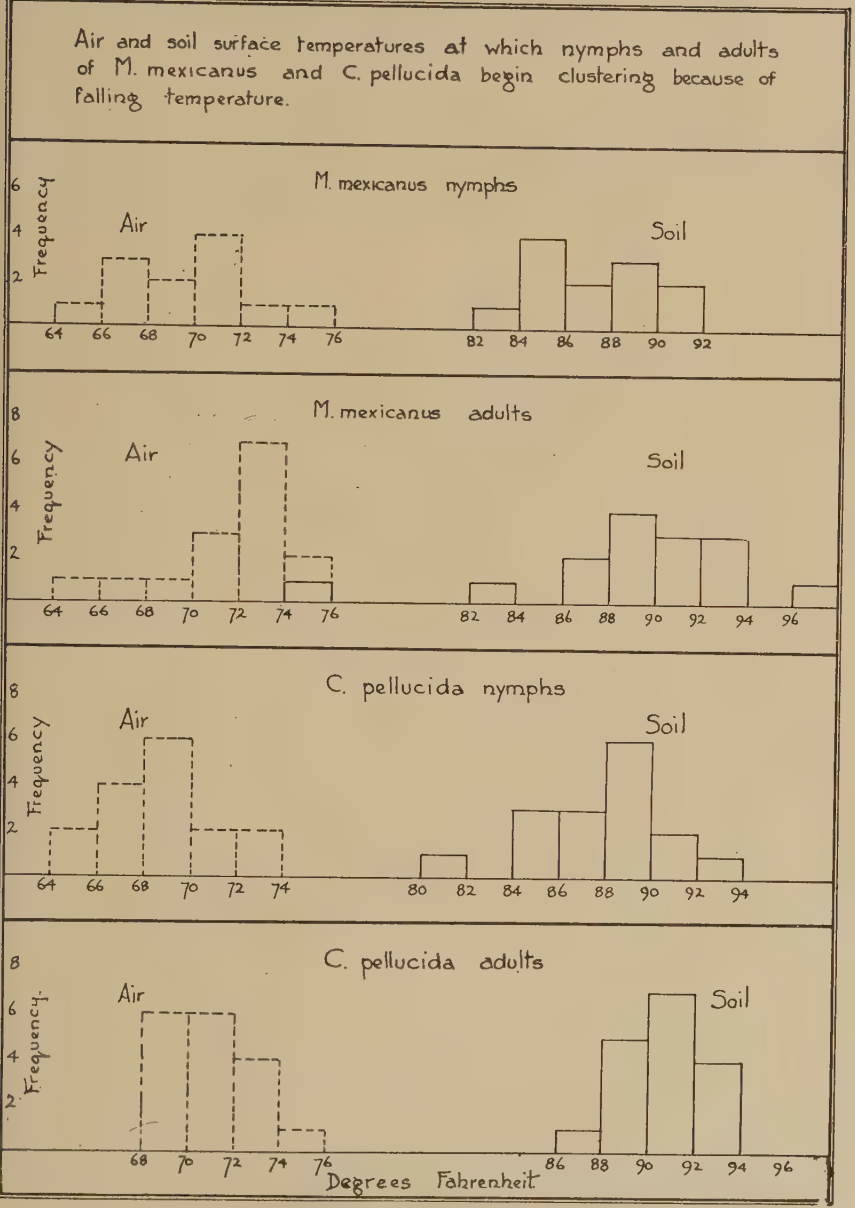
Air and soil surface temperatures at which nymphs and adults of M. mexicanus and C. pellucida begin clustering because of falling temperature.
M. mexicanus nymphs
Frequency
Air
Soil
64 66 68 70 72 74 76
82 84 86 88 90 92
M. mexicanus adults
Air
Soil
64 66 68 70 72 74 76
82 84 86 88 90 92 94 96
C. pellucida nymphs
Air
Soil
64 66 68 70 72 74
80 82 84 86 88 90 92 94
C. pellucida adults
Air
Soil
68 70 72 74 76
86 88 90 92 94 96
Degrees Fahrenheit

Figure 15

TABLE 32.—Air and soil surface temperatures at which nymphs and adults of **M. mexicanus** begin "clustering" because of falling temperatures.

Nymphs				Adults			
Place	Date	Air temp.	Soil temp.	Place	Date	Air temp.	Soil temp.
Valier, Mont.	5/23/24	68° F.	84° F.	Willow Cr'k, Mont.	6/23/24	73° F.	91° F.
Willow Cr'k, Mont.	6/2/24	66	86	" "	6/24/24	65	88
" "	6/3/24	70	88	" "	6/27/24	72	90
" "	6/10/24	66	84	" "	6/28/24	72	93
" "	6/11/24	65	90	" "	7/7/24	72	93
" "	6/12/24	67	85	" "	7/8/24	71	92
" "	6/13/24	70	88	" "	7/11/24	72	88
" "	6/14/24	72	86	" "	7/12/24	70	90
" "	6/16/24	68	89	" "	7/16/24	73	82
" "	6/17/24	70	90	" "	7/17/24	74	88
" "	6/20/24	71	82	" "	7/19/24	66	96
" "	6/21/24	74	84	" "	7/21/24	72	87
				" "	7/23/24	68	86
				" "	8/4/24	74	88
				" "	8/5/24	71	75
	Average	68.9	86.6		Average	71.0	88.4

TABLE 33.—Air and soil surface temperatures at which nymphs and adults of **C. pellucida** begin "clustering" because of falling temperatures.

Nymphs				Adults			
Place	Date	Air temp.	Soil temp.	Place	Date	Air temp.	Soil temp.
Lakeview, Mont.	6/21/20	68° F.	85° F.	Lakeview, Mont.	8/20/20	71° F.	92° F.
" "	6/22/20	69	88	" "	8/21/20	73	89
" "	6/23/20	72	84	" "	8/22/20	68	90
" "	6/24/20	72	88	" "	8/23/20	70	88
" "	6/25/20	67	90	" "	8/24/20	71	92
Harney, Minn.	6/28/23	69	86	" "	8/25/20	72	90
" "	6/29/23	66	92	Harney, Minn.	7/9/23	69	86
" "	6/30/23	65	89	" "	7/10/23	68	91
" "	7/1/23	67	88	" "	7/11/23	70	90
" "	7/2/23	66	86	" "	7/12/23	68	89
Minnie Lake, B. C.	6/4/25	64	80	Bozeman, Mont.	7/20/25	74	90
Bozeman, Mont.	6/18/25	71	87	" "	7/21/25	69	92
" "	6/19/25	70	88	" "	7/23/25	72	88
" "	6/20/25	69	89	" "	7/24/25	70	91
" "	6/24/25	68	91	" "	7/25/25	68	90
" "	6/25/25	69	84	" "	8/3/25	72	88
				" "	8/4/25	70	92
	Average	68.2	87.1		Average	70.3	89.8

C.) and the highest 72° F. (22.2° C.), the average being 68.2° F. (20.1° C.). Ten out of a total of 16 observations ranged from 66° to 69° F. (18.9° to 20.6° C.). The lowest soil surface temperature was 80° F. (26.7° C.) and the highest 92° F. (33.3° C.), the average being 87.1° F. (30.6° C.). Twelve out of a total of 16 observations ranged from 84° to 89° F. (28.9° to 31.7° C.).

In adults of the same species the lowest air temperature at which "beginning of clustering" was noted was 68° F. (20° C.) and the highest 74° F. (23.3° C.), the average being 70.3° F. (21.3° C.). Twelve out of a total of 17 observations ranged from 68° to 71° F. (20° to 21.7° C.). The lowest soil surface temperature was 86° F. (30° C.) and the highest 92° F. (33.3° C.), the average being 89.8° F. (32.1° C.). Twelve out of a total of 17 observations ranged from 88° to 91° F. (31.1° to 32.8° C.).

Temperatures at "Ending of Activity"

If the temperature continues to drop after grasshoppers have "clustered" in the warmer locations, the clusters finally break and the individual hoppers disappear from sight into various types of hiding places which are slightly warmer than open air. If no protection is available the grasshoppers remain clustered on the surface of the ground. Activity is considered at an end either when the majority of the grasshoppers have disappeared from sight or when all movements have ceased among the "clusters" on the surface of the ground.

Air and soil surface temperatures at which "ending of activity" was noted are given in Tables 34 and 35 and their frequency distribution is shown in Figure 16.

TABLE 34.—Air and surface temperatures at which "ending of activity" was noted in nymphs and adults of M. mexicanus.

Nymphs				Adults			
Place	Date	Air temp.	Soil temp.	Place	Date	Air temp.	Soil temp.
Valier, Mont.	5/23/24	65° F.	76° F.	Willow Cr'k, Mont.	6/23/24	71° F.	75° F.
Willow Cr'k, Mont.	6/2/24	64	74	" "	6/24/24	65	84
" "	6/3/24	66	78	" "	6/27/24	68	77
" "	6/10/24	63	76	" "	6/28/24	69	78
" "	6/11/24	63	80	" "	7/7/24	68	87
" "	6/12/24	65	79	" "	7/8/24	69	80
" "	6/13/24	67	78	" "	7/11/24	70	77
" "	6/14/24	68	76	" "	7/12/24	68	76
" "	6/16/24	64	77	" "	7/16/24	70	77
" "	6/17/24	66	75	" "	7/17/24	70	78
" "	6/20/24	70	76	" "	7/19/24	64	84
" "	6/21/24	71	75	" "	7/21/24	70	80
				" "	7/23/24	67	81
				" "	8/4/24	71	74
				" "	8/5/24	69	70
	Average	66	76.6		Average	68.6	78.5

TABLE 35.—Air and soil surface temperatures at which "ending of activity" was noted in nymphs and adults of **C. pellucida.**

Nymphs				Adults			
Place	Date	Air temp.	Soil temp.	Place	Date	Air temp.	Soil temp.
Lakeview, Mont.	6/21/20	66° F.	78° F.	Lakeview, Mont.	8/20/20	67° F.	76° F.
" "	6/22/20	66	80	" "	8/21/20	70	80
" "	6/23/20	65	78	" "	8/22/20	66	80
" "	6/24/20	65	79	" "	8/23/20	67	79
" "	6/25/20	64	79	" "	8/24/20	66	82
Harney, Minn.	6/28/23	66	77	Harney, Minn.	7/9/23	66	78
" "	6/29/23	64	82	" "	7/10/23	65	83
" "	6/30/23	63	78	" "	7/11/23	66	81
" "	7/1/23	65	78	" "	7/12/23	64	79
" "	7/2/23	64	80	Bozeman, Mont.	7/20/25	68	82
Minnie Lake, B. C.	6/4/25	60	70	" "	7/21/25	66	78
" "	6/5/25	60	64	" "	7/23/25	68	80
Bozeman, Mont.	6/18/25	67	77	" "	7/24/25	67	81
" "	6/19/25	66	78	" "	7/25/25	66	78
" "	6/20/25	65	80	" "	8/3/25	69	79
" "	6/24/25	66	78	" "	8/4/25	68	80
" "	6/25/25	66	76				
	Average	64.6	77.2		Average	66.8	79.8

In nymphs of *M. mexicanus* the lowest air temperature at which "ending of activity" was noted was 63° F. (17.2° C.) and the highest 71° F. (21.7° C.), the average being 66° F. (18.9° C.). Nine out of a total of 12 observations ranged from 62° to 67° F. (16.7° to 19.4° C.). The lowest soil surface temperature was 74° F. (23.3° C.) and the highest 80° F. (26.7° C.), the average being 76.6° F. (24.8° C.). Eleven out of a total of 12 observations ranged from 74° to 79° F. (23.3° to 26.1° C.).

In adults of the same species the lowest air temperature at which "ending of activity" was noted was 64° F. (17.8° C.) and the highest 71° F. (21.7° C.), the average being 68.6° F. (20.3° C.). Twelve out of a total of 15 observations ranged from 68° to 71° F. (20° to 21.7° C.). The lowest soil surface temperature was 70° F. (21.1° C.) and the highest 87° F. (30.6° C.), the average being 78.5° F. (25.8° C.). Nine out of a total of 15 observations ranged from 76° to 81° F. (24.4° to 27.2° C.).

In nymphs of *C. pellucida* the lowest air temperature at which "ending of activity" was noted was 60° F. (15.6° C.), and the highest 67° F. (19.4° C.), the average being 64.6° F. (18.1° C.). Fourteen out of a total of 17 observations ranged

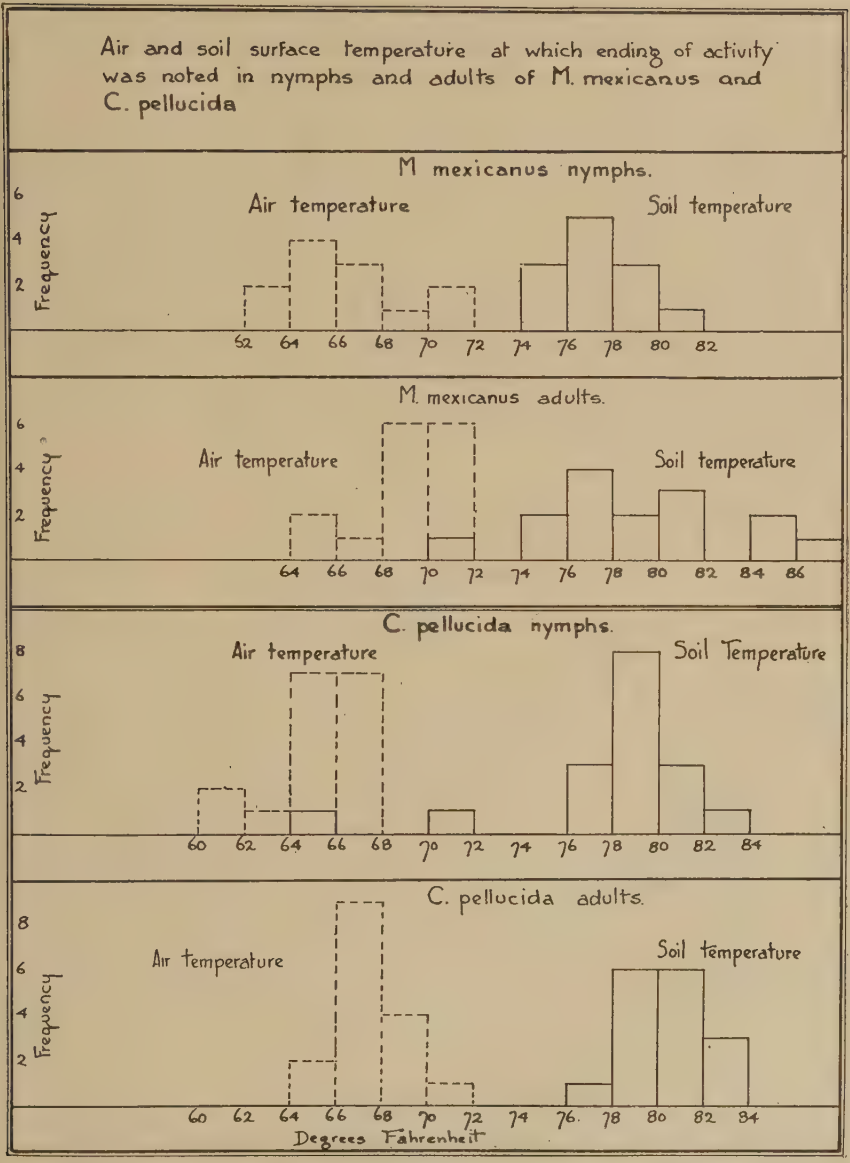
Air and soil surface temperature at which ending of activity was noted in nymphs and adults of M. mexicanus and C. pellucida
M mexicanus nymphs.
Air temperature
Soil temperature
Frequency
6
4
2
52 64 66 68 70 72 74 76 78 80 82
M. mexicanus adults.
Air temperature
Soil temperature
Frequency
6
4
2
64 66 68 70 72 74 76 78 80 82 84 86
C. pellucida nymphs.
Air temperature
Soil Temperature
Frequency
8
6
4
2
60 62 64 66 68 70 72 74 76 78 80 82 84
C. pellucida adults.
Air temperature
Soil temperature
Frequency
8
6
4
2
60 62 64 66 68 70 72 74 76 78 80 82 84
Degrees Fahrenheit

Figure 16

from 64° to 67° F. (17.8° to 19.4° C.). The lowest soil surface temperature was 64° F. (17.8° C.) and the highest 82° F. (27.8° C.), the average being 77.2° F. (25.1° C.). Fourteen out of a total of 17 observations ranged from 76° to 81° F. (24.4° to 27° C.).

In adults of the same species the lowest air temperature at which "ending of activity" was noted was 64° F. (17.8° C.) and the highest 70° F. (21.1° C.), the average being 66.8° F. (19.3° C.). Thirteen out of a total of 16 observations ranged from 66° to 69° F. (18.9° to 20.6° C.). The lowest soil temperature was 76° F. (24.4° C.) and the highest 82° F. (27.8° C.), the average being 79.8° F. (26.6° C.). Twelve out of a total of 16 observations ranged from 78° to 81° F. (25.6° to 27.2° C.).

TEMPERATURES AT WHICH ACTIVITIES TAKE PLACE IN TEMPERATURE CABINETS

Activities During Changing Temperatures

In order to determine the temperature limits of activity under controlled conditions, several hundred adults of *C. pellucida* and a smaller number of *M. mexicanus* adults were confined in a Carrier Air Conditioning Cabinet, the bottom of which was covered with clumps of green grass. Starting from a temperature of 25° C. (77° F.) the temperature was lowered at the rate of about 1° C. in two minutes. Feeding perceptibly slowed down at 20° C. (68° F.) but slight feeding continued until a temperature of 10° C. (50° F.) was reached. Below this temperature the grasshoppers remained motionless and at 3° C. (37.4° F.) were completely dormant. After 30 minutes' exposure to 0° C. (32° F.) the temperature was allowed to rise at the rate of about 1° C. in 5 minutes. At 7° C. (44.6° F.) slight movements of antennae could be detected; at 9° C. (48.2° F.) movements of legs were seen; at 10° C. (50° F.) individuals that had been on their backs and sides were resuming a natural position; at 12° C. (53.6° F.) some were beginning to crawl; at 15° C. (59° F.) many were crawling from beneath the grass and moving about quite generally. At 17° C. (62.6° F.) slight feeding began and gradually increased as the temperature rose; at 27° C. (80.6° F.) practically every grasshopper was either

feeding vigorously, laying eggs, or mating. As the temperature continued to rise all activities continued at a still faster pace until a temperature of 47° C. (116.6° F.) was reached. At this temperature many females were frenziedly laying eggs but feeding had stopped and all grasshoppers were excited and nervous and many were attempting to fly as if to escape the heat. The upper limit of normal activity, therefore, is approximately 46° C. (114.6° F.). Slight differences in the temperature limits of the two species were noted. Both showed signs of activity at about the same temperature but *M. mexicanus* was more actively feeding at 25° C. (77° F.) than was *C. pellucida,* and also started egg laying at that temperature while egg laying in *C. pellucida* did not start until a temperature of 27° C. (80.6° F.) was reached. At high temperatures *C. pellucida* ceased active feeding at a slightly lower temperature than *M. mexicanus.*

Other similar experiments were conducted with nymphs of both species. On a falling temperature nymphs of *C. pellucida* ceased all feeding at 17° C. (62.6° F.) while *M. mexicanus* nymphs in the same cabinet continued to feed until a temperature of 11° C. (51.8° F.) was reached, below which temperature both species became entirely inactive.

When the temperature was allowed to rise again, first movements of antennae were seen in *M. mexicanus* at 6° C. (42.8° F.) and in *C. pellucida* at 8° C. (46.4° F.). At 10° C. (50° F.) some individuals of both species were starting to crawl. *M. mexicanus* started to feed at 16° C. (60.8° F.) while in *C. pellucida* no feeding was noticed until the temperature reached 18° C. (64.4° F.). At 24° C. (75.2° F.) both species were feeding quite generally and continued to feed until a temperature of approximately 45° C. (113° F.) was reached. At this point they became greatly excited, jumping and crawling frantically about in an attempt to find a cooler location.

Activities at Constant Temperatures

Nymphs and adults of *M. mexicanus* held at constant temperatures of 8° and 12° C. (46.4° and 53.6° F.) lived for several weeks but never fed. Both nymphs and adults nibbled at vegetation occasionally at 16° C. (60.8° F.) and fed fairly regularly at 19° C. (66° F.) but at this temperature the nymphs

never molted. At 22° C. (71.6° F.) feeding increased slightly over that at 19° C. (66° F.) and some of the nymphs were able to molt. However, many of those that molted were abnormal, and out of several thousand first instar nymphs started at this temperature less than a hundred were ever reared to maturity. The lower limit of normal development, therefore, is 22° C. (71.6° F.).

In connection with experiments made to determine the lowest temperatures at which feeding took place, it was found that in the narrow zone where temperature is barely high enough to bring about slight feeding and activity, death always occurred sooner than at low temperatures where there was no feeding and at higher temperatures where normal activities were taking place. This was checked several times and the results of one of the experiments are shown in Table 36.

TABLE 36.—Death rate of M. mexicanus nymphs at constant temperatures of 8°, 12°, 16° and 19° C. Twenty nymphs in each lot.

	8°		12°		16°		19°	
Days	Dead	Feeding	Dead	Feeding	Dead	Feeding	Dead	Feeding
1	0	None	0	None	0	Yes	0	Yes
2	0	"	0	"	0	"	0	"
3	0	"	0	"	0	"	0	"
4	0	"	0	"	0	"	8	"
5	0	"	1	"	1	"	5	"
6	0	"	1	"	4	"	4	"
7	0	"	0	"	5	"	0	"
8	0	"	0	"	0	"	1	"
9	1	"	1	"	7	"	1	"
10	0	"	0	"	1	None	0	"
11	2	"	6	"	0	"	0	"
12	3	"	1	"	2	"	1	"
13	6	"	3	"				
14	1	"	1	"				
15	4	"	4	"				
16	0	"	0	"				
17	3	"	2	"				

The table shows that at 8° and 12° C. (46.4° and 53.6° F.) no deaths occurred before 10 days and some lived for 17 days. At 16° and 19° C. (60.8° and 66° F.) half of the nymphs were dead at the end of 7 days and none lived over 12 days. This suggests a possible explanation of the high death rate among young grasshoppers when unseasonably warm weather causes the eggs to hatch early in the spring. Very cool weather usu-

ally follows, during which the young hoppers are kept on the border line of inactivity for days at a time.

Nymphs and adults of *C. pellucida* did not feed at 16° C. (60.8° F.) but fed sparingly at 19° C. (66° F.). At 20° C. (68° F.) the nymphs feed and become quite plump but never molt. If, after being held at this temperature for some time, they are placed at a high temperature they molt within a few minutes. At 22° C. (71.6° F.) some molting takes place, but out of hundreds of *C. pellucida* nymphs started at this temperature none ever produced normal adults. Perfectly normal development takes place at 27° C. (80.6° F.). The lower limit of normal development is probably about 24° C. (75.2° F.).

The upper limit of normal development for both *M. mexicanus* and *C. pellucida* is approximately 37° C. (98.6° F.). The death rate in the early instars is very high at this temperature, especially in *C. pellucida,* but many adults of both species have been reared. The later instars and adults of *M. mexicanus* will live for several weeks at 38° C. (100° F.), being slightly more heat resistant than *C. pellucida.*

Egg laying of *M. mexicanus* rarely took place at 22° C. (71.6° F.) but was common at 27° C. (80.6° F.) and above. In *C. pellucida,* egg laying practically never occurred at 22° C. (71.6° F.) and rarely at 27° C. (80.6° F.) but took place frequently at higher temperatures. The number of egg masses produced at different temperatures will be discussed in a later section of this paper.

EFFECT OF LOW TEMPERATURE

Second and third instar nymphs of both *M. mexicanus* and *C. pellucida* survived a 24-hour exposure to –7° C. (19.4° F.). At –8° C. (17.6° F.) about 50 per cent survived a 24-hour exposure but all were killed by a 48-hour exposure.

When adults of these two species were placed in a Carrier Cabinet and the temperature lowered at the rate of about 1° C. every 5 minutes, they became completely motionless at 3° C. (37° F.) but at –3° C. (26.6° F.) again became active and started to jump about in much the same manner as when exposed to high temperatures which are above the limit of normal activity. Between –4° and –6° C. (24.8° and 21.2° F.) they

dragged their legs as if partially paralyzed and some fell on their sides and back in cold rigor. At –8° C. (17.6° F.) all were on their backs or sides perfectly motionless. The temperature was lowered to –12° C. (10.4° F.) where it was held for one hour, and then allowed to rise gradually to room temperature. Out of 10 specimens of each species, 7 of *M. mexicanus* and 2 of *C. pellucida* survived.

Adults of *M. mexicanus* survived a 24-hour exposure at –9° C. (15.8° F.), but 15 out of 20 specimens were killed by a 48-hour exposure. At –10° C. (14° F.) all were killed by a 24-hour exposure.

Adults of *C. pellucida* survived a 24-hour exposure at –8° C. (17.6° F.) but 12 out of 20 specimens were killed by a 48-hour exposure. At –9° C. (15.8° F.) all were killed at a 24-hour exposure.

Twelve adults of *M. mexicanus* were packed in snow and held at a temperature of 0° C. (32° F.). Each day they were removed to a warm room where they were held until they became active, after which they were again packed in snow and returned to cold storage. On the tenth day one specimen was found dead, 8 died on the fourteenth day, and the remaining 3 died on the eighteenth day.

From the foregoing it may be expected that both nymphs and adults of *M. mexicanus* and *C. pellucida* would survive 24-hour exposures at any low temperatures above –7° C. (19.4° F.) but would be killed by a 24-hour exposure at –10° C. (14° F.) or below. It is also apparent that adult grasshoppers would not be killed by snow storms which sometimes occur in Montana during the period of adult life. During May, 1924, *M. mexicanus* hatched in great numbers in Teton County, Montana, and about a week after hatching was subjected to 5 inches of snow, which remained on the ground in many places for 48 hours. After the snow had melted the young grasshoppers were perfectly normal and the death rate was no higher than in localities in the same county where there had been no snow.

EFFECT OF HIGH TEMPERATURE

Nymphs of *M. mexicanus* and *C. pellucida* when confined in temperature cabinets became greatly excited when the tem-

perature reached 45° to 47° C. (113° to 116° F.), jumping and crawling frantically about. When the temperature is raised above this point at the rate of 1° C. in every 5 minutes, first signs of heat rigor are noted at 49° to 52° C. (120° to 125.6° F.). This is indicated by paralysis of the legs, followed by falling on side or back. At 53° to 54° C. (127.4° to 129.2° F.) all specimens are in complete heat rigor. If they are immediately removed to room temperature many of them will frequently recover, but a 10-minute exposure at 54° C. (129.2° F.) always results in death. No definite difference in heat resistance could be found between the two species.

Adults of *M. mexicanus* and *C. pellucida* became excited at the same temperature as nymphs, 45° to 47° C. (113° to 116° F.), the latter species generally showing nervousness slightly in advance of the former. First signs of heat rigor appear at temperatures of 52° to 54° C. (125.6° to 129.2° F.). At 56° to 58° C. (132.8° to 136.4° F.) all specimens are generally in complete heat rigor. If removed immediately to room temperature many females will recover but only an occasional male. A 10-minute exposure at 58° C. (136.4° F.) always resulted in death.

EFFECT OF TEMPERATURE UPON THE AMOUNT OF FOOD CONSUMED

Experiments were conducted with *M. mexicanus* to determine the exact amount of food consumed at different temperatures. Grasshoppers were confined in glass tubes 8 inches long and 1½ inches in diameter, one end being closed with cheesecloth and the other with brass screening. Ten grasshoppers were kept in each tube. Following a suggestion from Norman Criddle, wandering jew *(Tradescantia)* was used as food and it proved most satisfactory. It is easily grown in quantity in the greenhouse and can be cut into small pieces which remain crisp and succulent in the rearing tubes for a 24-hour period. Circular pieces, each containing 0.371 square inch, were cut with a cork borer. These were fed slightly in excess of the daily need, any food remaining in the tubes at the end of the 24-hour period being carefully removed and its dry weight determined. Each day 50 disks of the current day's food supply were taken as samples and their dry weight determined. From this the

average weight of dry matter per disk was computed, and by multiplying this amount by the number of disks fed and subtracting the dry weight of the food remaining in the tube, the amount of dry matter consumed daily by the grasshoppers in any one tube could be easily determined.

Amount of Food Consumed at Constant Temperatures During the Nymphal Stage

Ten individuals of *M. mexicanus* were carried from the time of hatching to the adult stage at each of the following constant temperatures, 22°, 27°, 32°, and 37° C. A few individuals died before the adult stage was reached but were replaced by others in the same stage of development, which had been grown on similar food and at the same temperature. The relative amounts of food (dry weight) consumed daily at the different temperatures are shown graphically in Figure 17, the curve for nymphal feeding in each case terminating at the point marked "A" (adult). At 37° and 32° C. the curves run very close together but at 27° and 22° C. there is a decided decrease in the daily amount of food consumed in each case as the temperature is lowered. In most cases all of the curves show decreased feeding just previous to the molting periods and a rather sharp increase directly after molting. This characteristic of the curves would be still more pronounced were it not for the fact that there was always a difference of several days between the molting of the first and the last individual in each instar, the molting points—"M" on the curve—representing only the average length of each instar.

Although the daily amounts of food consumed differ widely, according to temperature differences, the total amount consumed during the nymphal stage is practically the same at all four temperatures. This fact is shown graphically in Figure 18, which also shows the relative length of the nymphal stage at each temperature. Although the nymphal period varies in length from 25 days at 37° C. to 94 days at 22° C., there is less than 5 per cent variation in the amount of food consumed.

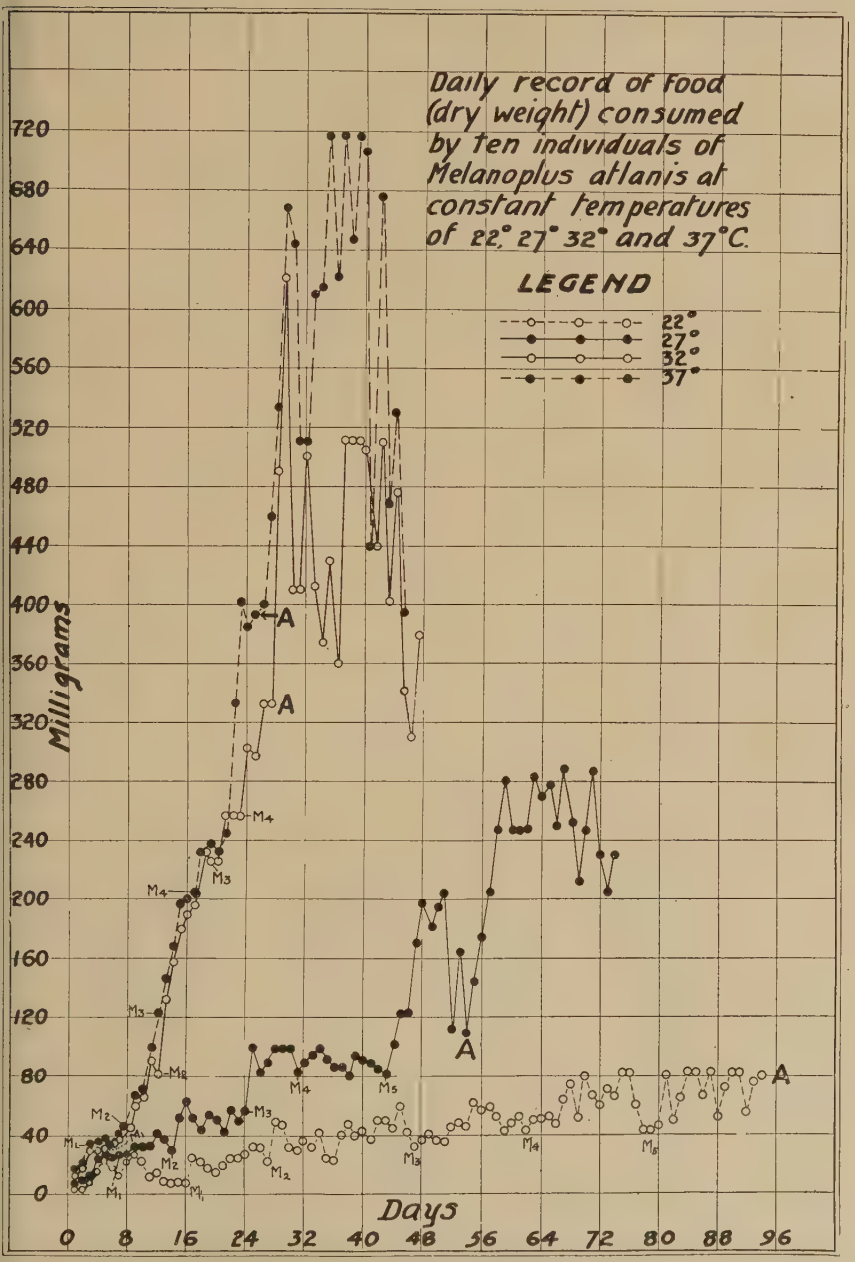
Daily record of food (dry weight) consumed by ten individuals of Melanoplus atlanis at constant temperatures of 22°, 27°, 32° and 37°C.
LEGEND
22°
27°
32°
37°
Milligrams
Days
0
40
80
120
160
200
240
280
320
360
400
440
480
520
560
600
640
680
720
0
8
16
24
32
40
48
56
64
72
80
88
96
A
M1
M2
M3
M4
M5
M6

Figure 17

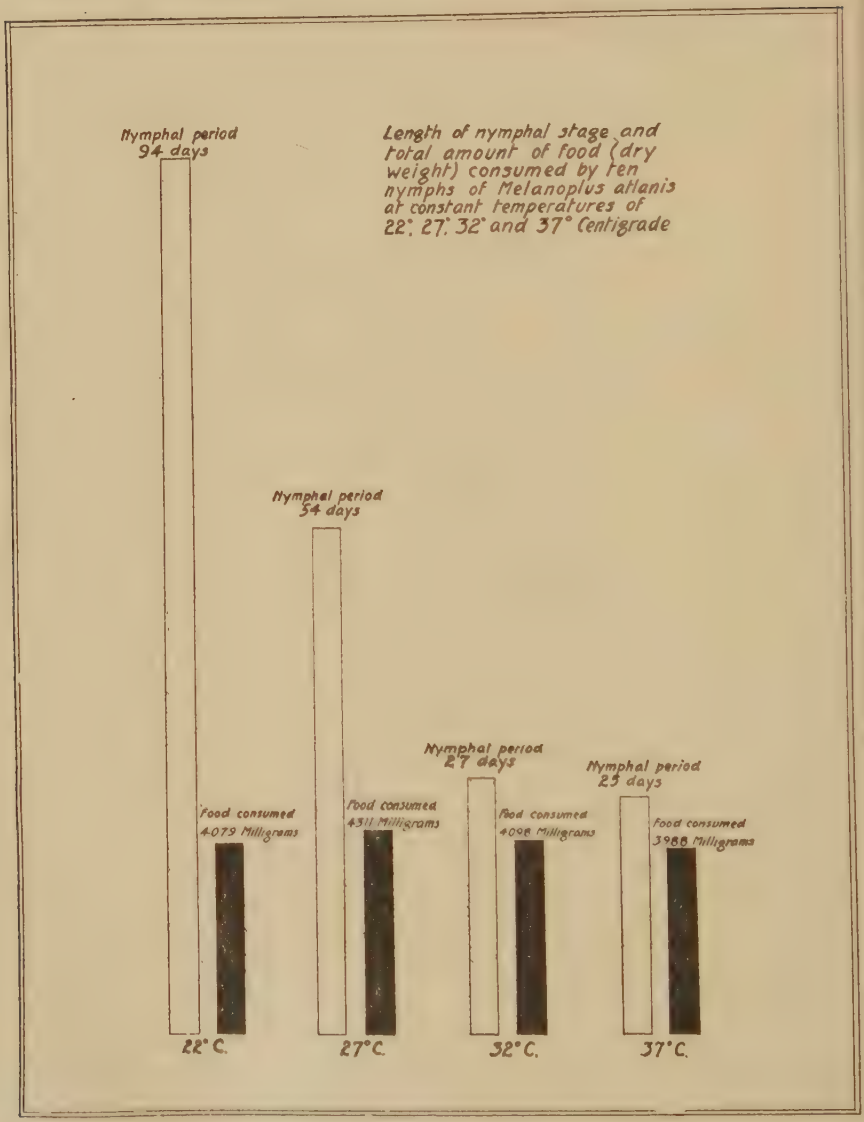
Length of nymphal stage and total amount of food (dry weight) consumed by ten nymphs of Melanoplus atlanis at constant temperatures of 22°, 27°, 32° and 37° Centigrade
Nymphal period 94 days
Food consumed 4.079 Milligrams
22° C.
Nymphal period 54 days
Food consumed 4.311 Milligrams
27° C.
Nymphal period 27 days
Food consumed 4.098 Milligrams
32° C.
Nymphal period 23 days
Food consumed 3.988 Milligrams
37° C.

Figure 18

Comparison of Amount of Food Consumed in the Nymphal Stage at Constant and Alternating Temperatures

A second feeding experiment was conducted with *M. mexicanus* nymphs held both at constant and at alternating tempera-

tures. Grasshoppers were held in tubes and fed in the same manner as in the first experiment. One series was held continuously at constant temperatures of 27°, 32°, and 37° C. while

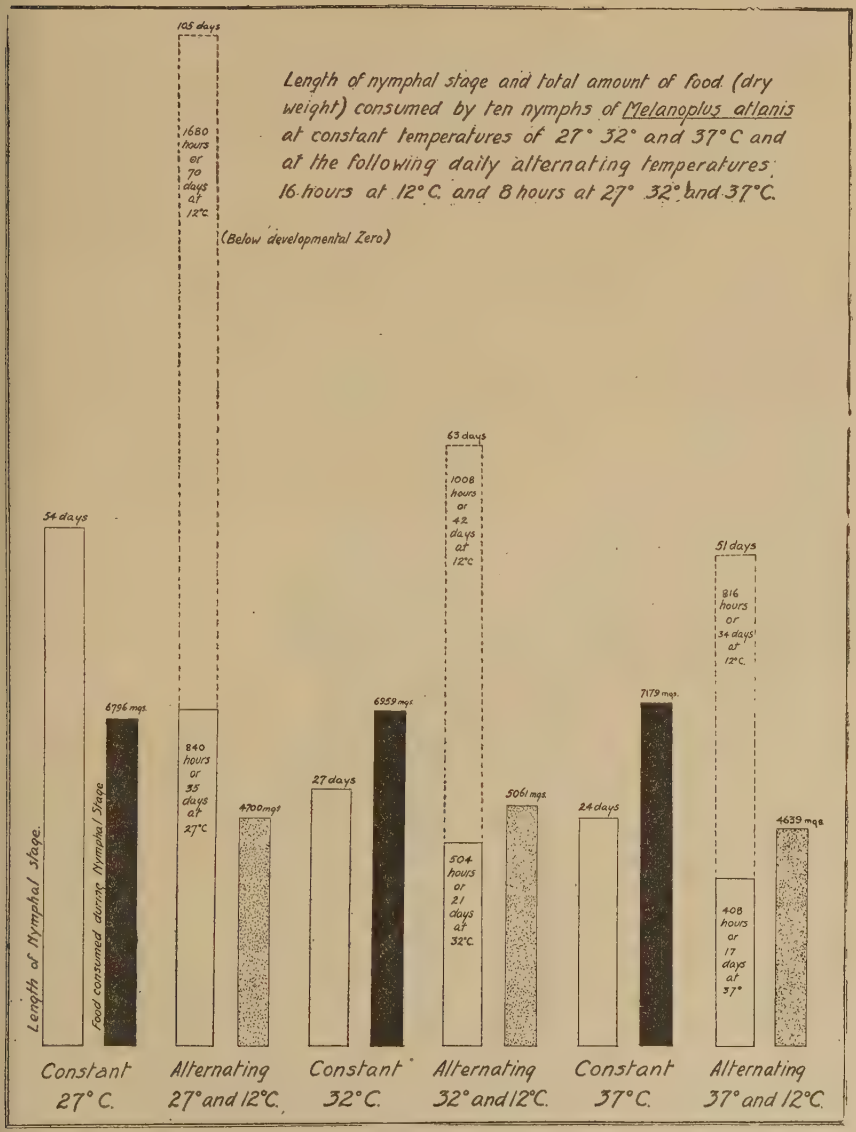
Length of nymphal stage and total amount of food (dry weight) consumed by ten nymphs of Melanoplus atlanis at constant temperatures of 27° 32° and 37° C and at the following daily alternating temperatures: 16 hours at 12° C. and 8 hours at 27° 32° and 37° C.
105 days
1680 hours or 70 days at 12°C
(Below developmental Zero)
54 days
6796 mgs.
840 hours or 35 days at 27°C
4700 mgs
27 days
6959 mgs.
63 days
1008 hours or 42 days at 12°C
504 hours or 21 days at 32°C.
5061 mgs.
24 days
7179 mgs.
51 days
816 hours or 34 days at 12°C.
408 hours or 17 days at 37°
4639 mgs.
Length of Nymphal stage.
Food consumed during Nymphal Stage
Constant 27° C.
Alternating 27° and 12°C.
Constant 32°C.
Alternating 32° and 12°C.
Constant 37°C.
Alternating 37° and 12°C.

Figure 19

another series was held for 8 hours daily at 27°, 32°, and 37° C. and for 16 hours at 12° C., which is below developmental zero. The results of this experiment are shown graphically in Figure 19, which also shows the length of the nymphal stage.

The amount of food consumed in the nymphal stage was approximately the same at the three constant temperatures, but there was a marked reduction in the amount of food consumed at alternating temperatures. For constant temperatures the dry weight of food consumed by 10 *M. mexicanus* nymphs was 6796 mgs. at 27° C., 6959 mgs. at 32° C. and 7179 mgs. at 37° C. These amounts are larger than for the same constant temperatures in the first feeding experiment. This is probably due to the fact that the grasshoppers in the first experiment were hatched from a different stock supply of eggs and were somewhat smaller. At alternating temperatures the dry weight of food consumed by 10 nymphs was 4700 mgs. at 27° and 12° C., 5061 mgs. at 32° and 12° C., and 4639 mgs. at 37° and 12° C. This amounts to a 24 per cent reduction from the amount of food used during the nymphal stage at constant temperatures. The average reduction in the length of the nymphal stage (not counting time at 12° C.) was 30 per cent.

From the foregoing it would seem that daily alternating temperatures are more favorable for growth, grasshoppers completing their nymphal stage in less time and on less food than at constant temperatures.

Effect of Temperature on Amount of Food Consumed by Adults

Experimental feeding at 27°, 32°, and 37° C. was carried on during the first 20 days of adult life with the same groups that had been fed at these temperatures during the nymphal stage. No record was available at 22° C. because a majority of the grasshoppers died while attempting the final molt, this temperature being too low for normal development. The relative amounts consumed daily are shown in those parts of the curves in Figure 17 lying to the right of the points marked "A." In general, it may be said that immediately after the adult stage is reached, daily food consumption increases rapidly, reaching its maximum in about a week, at which time it may be from 50 to 75 per cent greater than during the last nymphal instar.

The effect of temperature upon feeding during this period can perhaps be best expressed by a comparison of the total amounts consumed at the different temperatures. This is shown graphically in Figure 20.

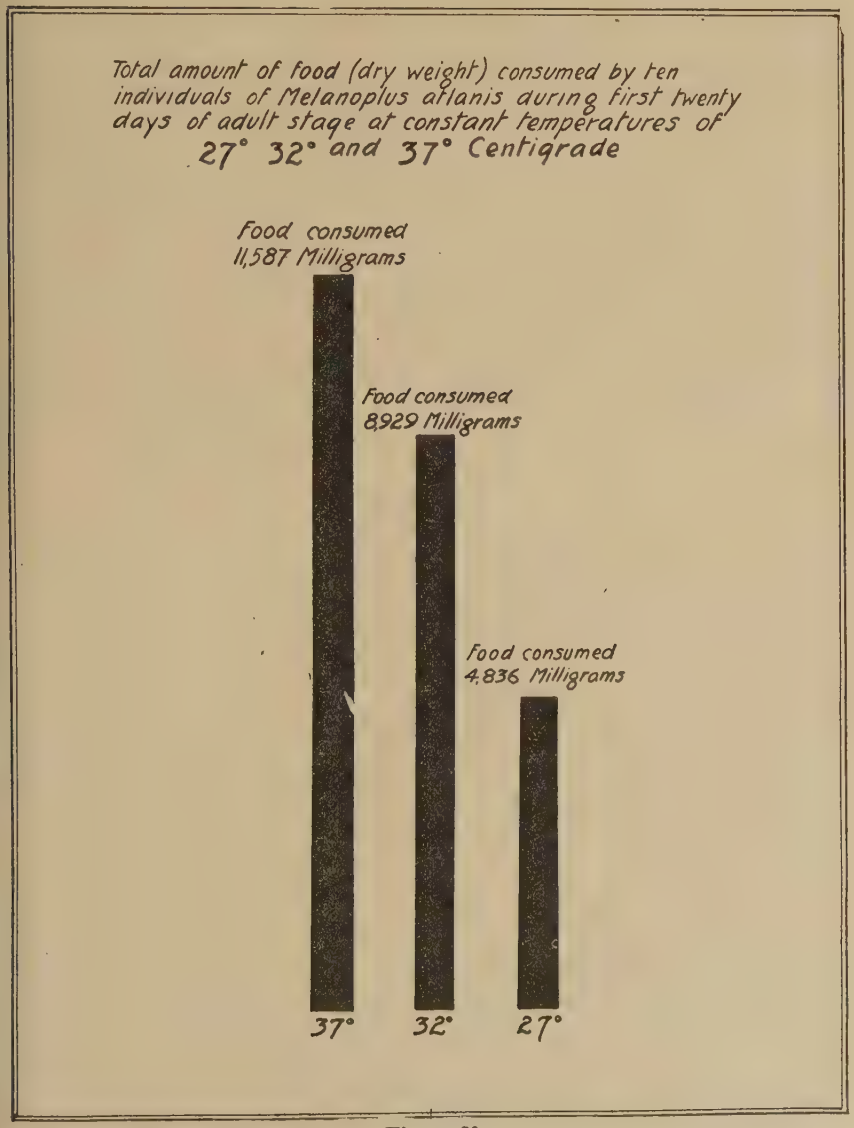
Total amount of food (dry weight) consumed by ten individuals of Melanoplus atlanis during first twenty days of adult stage at constant temperatures of 27° 32° and 37° Centigrade
Food consumed 11,587 Milligrams
Food consumed 8,929 Milligrams
Food consumed 4,836 Milligrams
37°
32°
27°

Figure 20

It will be noted that 10 grasshoppers held at 37° C. consumed 11,587 mgs. of dry matter, or nearly 2.5 times as much as the amount consumed by an equal number at 27° C.

The effect of changes in temperature upon food consumption was determined as follows: Four groups, each composed of 5 males and 5 females of *M. mexicanus*, were used. On the first day one group was placed at each of the four constant temperatures, 37°, 32°, 27°, and 22° C. At the end of the 24-hour period the group at 37° was transferred to the 22° cabinet and the other three groups were each advanced to a cabinet 5° warmer. Similar rotations were made every 24 hours over a period of 20 days. Food consumption in all four groups varied with the temperature, a difference of 10° C. increasing or decreasing the food consumption two or three-fold. The daily differences at the different temperatures are shown graphically in Figure 21.

If the feeding records at each of the four constant temperatures are added, it is found that the dry weight of food consumed in 20 days at each temperature was as follows:

37° C.—7010 milligrams
32° C.—5160 milligrams
27° C.—3120 milligrams
22° C.—1740 milligrams

These amounts are somewhat smaller than those shown in Figure 20 for equal periods and temperature, but this can be partly explained by the fact that in the first experiment the first 20 days of adult life were included, while in the latter the grasshoppers became adult 10 days before the experiment started, which resulted in a more rapid falling off in feeding toward the end of the 20-day period.

If the amounts of food consumed at 37° and 32° and 27° in the last experiment are averaged and reduced to milligrams per hour per grasshopper, it is found that one grasshopper at 27° to 37° eats 1 mg. of dry matter per hour. Since *Tradescantia* contains 6 per cent of dry matter, the amount of green food per grasshopper per hour would be 16.6 mgs. An adult of *M. mexicanus* weighs from 250 to 300 mgs. and will therefore at these temperatures eat its own weight in green food every 15 to 18 hours. On the Fahrenheit scale these tempera-

tures correspond very closely to 80° and 100°. Field observations have shown that these temperatures exist most commonly within the 2-inch zone directly above the ground (the space where grasshoppers are found) when air temperatures as recorded in an instrument shelter 4 feet above the ground are registering from 70° to 80° F. It therefore may be assumed that on days when the air temperature at 4 feet ranges from

Relative amounts of food (dry weight) consumed by ten adults of Melanoplus atlanis when held for daily periods at different constant temperatures. Experiment conducted in quadruplicate.
1
2
3
4

Figure 21

70° to 80° F. each grasshopper will eat at least 1 mg. of dry matter per hour. This figure is undoubtedly too low since it is based on data obtained in constant temperature cabinets where feeding took place throughout the 24 hours instead of following a rest period as in nature, but it will do as a basis for comparison.

Field observations have shown that feeding activities are greatest when the air temperature at 4 feet is between 70° and 80° F. (21.1° and 26.7° C.), feeding decreasing rapidly both below and above these temperatures. Turning to the official weather records for Bozeman during the period from July 10 to October 1, 1918, it is found that there were only 193 hours when the temperature ranged between these two favorable points, while in 1919 there were 418. The amount of dry matter consumed per grasshopper was therefore 193 mgs. in 1918 and 418 mgs., or 2.2 times as much, in 1919. It is therefore not surprising that grasshopper damage should be most severe during periods of high temperature, for even though there were no increase in numbers, the damage to crops might be doubled because of the greater amount of food each grasshopper would consume at the higher temperature.

EFFECT OF TEMPERATURE UPON REPRODUCTION

How Many Egg Masses Are Laid by One Female

Very little published data can be found on the number of egg masses laid by a female grasshopper in one season. The most definite statement is that given by Riley (14) who says—"With *spretus* I have been able to make comparatively few experiments; but on three different occasions I obtained two pods from single females. I have, however, made extended experiments with its close congeners, *femur-rubrum* and *atlanis (mexicanus)*, and in two cases with the former have obtained 4 different pods from one female. A number of both species laid three times but most of them, owing, perhaps, to their being confined, laid but twice." This statement has apparently been accepted without further question by more recent students of Orthoptera, nearly all papers dealing with economic species stating that each female lays only two egg masses per season. In no instance, aside from Riley's statement, have I been able

to find any record in American entomological literature of four or more egg masses per female.

A knowledge of the number of egg masses laid by one female is of considerable importance in connection with the effect of temperature upon grasshopper abundance. If two or three egg masses were all that one female was capable of laying she would doubtless, at some time during the summer months, find the necessary favorable temperature conditions for depositing her full quota of eggs, and changes in temperature would have but little effect on the total number laid. If, on the other hand, eggs are developed and deposited throughout the summer, as long as temperature conditions are favorable, the total number deposited would then depend to a considerable extent upon the temperature factor.

An experiment to determine whether the maximum of three egg masses per female reported for *M. mexicanus* by Riley was ever exceeded, was conducted in 1924. Pairs of this species were collected in the field early in August and isolated in lamp chimney cages placed over flower pots containing packed sand. The cages were kept in a well-lighted laboratory where the temperature averaged approximately 75° F. The sand in each flower pot was searched for egg pods every 24 hours by passing it through a coarse screen. Fifty pairs were caged but, owing to parasitism and injuries received in handling, some of these died shortly after being caged. Records are given only for those that lived at least three weeks after being caged. The record of egg masses laid is shown in Table 37.

In view of the fact that other workers never suggested the possibility of more than 4 egg masses being laid by one female, the results were surprising. With but two exceptions, every female exceeded this number; one female deposited 15 egg masss and the average for 30 females was 8.8 laid at average intervals of four to five days. The number of eggs per mass varied from 12 to 36, but averaged no higher for females laying a few pods than for those laying many. The average of 25 eggs per mass is twice the number found by Herrick and Hadley (7) for the same species in New York.

It should be pointed out that the grasshoppers used in the experiment were collected in the field on August 10, which was

at least two or three weeks after most of them had reached maturity, and there is no doubt that some of them had already laid eggs before they were caged. Had they been caged earlier an even greater number of egg masses per female would have been obtained.

TABLE 37.—Number of egg masses laid by **M. mexicanus** females collected in the field during August, and held in cages at room temperature (21° to 27° C.) (69.8° to 80.6° F.).

Female number	Days alive in cage	Egg masses laid	Days in cage per egg mass	Female number	Days alive in cage	Egg masses laid	Days in cage per egg mass
1	40	10	4.0	16	30	6	5.0
2	42	11	3.8	17	47	12	7.4
3	60	14	4.2	18	47	10	4.7
4	52	10	5.2	19	31	7	4.4
5	46	12	3.8	20	50	12	4.1
6	25	4	6.2	21	60	15	4.0
7	45	8	5.0	22	34	4	8.5
8	40	10	4.0	23	56	13	4.3
9	22	5	4.4	24	41	9	4.5
10	20	5	4.0	25	52	12	4.3
11	44	6	7.3	26	44	7	6.3
12	34	8	4.2	27	50	9	5.5
13	26	5	5.2	28	56	10	5.6
14	42	13	3.2	29	30	5	6.0
15	40	6	6.6	30	30	7	4.2
				Average	41.2	8.8	4.9

In 1927, pairs of *M. mexicanus* were collected in the field on September 23 and held at room temperature until they died. The average number of egg pods per female was 5, and the average length of life in the cages was 30 days. However, one female lived from September 23 to December 2, a period of 70 days during which time 11 egg pods were laid. In view of the fact that egg laying had been taking place at least two months previous to the time when females were caged, it seems reasonable to believe that vigorous females may each have a potential capacity of 20 egg pods.

Females reared from the egg under artificial conditions in constant temperature cabinets would not be expected to be as vigorous or productive as females under natural outdoor conditions. However, 10 pairs of reared *M. mexicanus* placed at a constant temperature of 37° C. one week after becoming adult, lived for 40 days and produced 95 egg pods, an average of almost 10 egg pods per female.

Effect of Temperature Upon Number of Egg Pods Laid

Having demonstrated that under favorable conditions egg laying can take place at frequent intervals over a period of several months, further experiments were undertaken to determine the effect of temperature upon the number of egg pods deposited. Pairs of *M. mexicanus* and *C. pellucida* were collected in the field during late August and held in lamp chimney cages at constant temperatures of 22°, 27°, 32°, and 37° C. The experiment was continued until all females were dead. The results are shown in Table 38.

TABLE 38.—Length of life in cage and number of egg pods deposited by **M. mexicanus** and **C. pellucida** when confined at constant temperatures of 22°, 27°, 32° and 37°. Ten pairs of field collected specimens held at each temperature.

	M. mexicanus				C. pellucida			
	22° C.	27° C.	32° C.	37° C.	22° C.	27° C.	32° C.	37° C.
Average number of days alive in cage	32.8	27.8	22.0	19.6	29.0	32.6	28.0	15.8
Average number of egg-pods per female	.4	7.8	8.0	6.0	.2	1.0	6.2	4.2

With *M. mexicanus* there was little difference in the number of egg pods deposited at 37°, 32°, and 27° C., the average being respectively 6, 8, and 7.8 per female. At 22° C. there was sharp reduction, the average being only 0.4 egg pod per female. The greatest number of egg pods laid by one female was 14 at 37° C., 10 at 32° C., 11 at 27° C., and 1 at 22° C.

With *C. pellucida* the average number of egg pods per female was 4.2 at 37° C. and 6.2 at 32° C., while at 27° C. it was reduced to 1, and at 22° C. to 0.2. The greatest number of egg pods laid by one female was 10 at 37° C., 11 at 32° C., 3 at 27° C., and 1 at 22° C.

From the foregoing it appears that temperatures ranging from 27° to 37° C. are favorable to optimum egg production by *M. mexicanus* and that *C. pellucida* has a narrower range, extending from 32° to 37° C.

Effects of Temperature Upon Grasshopper Abundance

Field observations have shown that *M. mexicanus* females start egg laying at an average air temperature of 71° F. (21.7° C.) and soil surface temperature of 100° F. (37.7° C.). A com-

bination of these air and soil surface temperatures should bring about temperature conditions in the zone just above the ground where grasshoppers are generally found, that would fall within the range of 27° to 37° C. (80° to 98.6° F.) which was found to be the optimum for egg laying in temperature cabinets. When confined at these temperatures *M. mexicanus* females deposited an average of one egg pod every 80 hours, and for a basis of comparison it is assumed that females will lay eggs at about the same rate whenever the air temperature goes above 71° F. (21.7° C.). The official weather record for Bozeman during the egg-laying period of *M. mexicanus* in 1918 (July 10 to October 1) shows that there were 264 hours when the air temperature was above 71° F. (21.7° C.). This would make possible an average of 3.3 egg masses per *M. mexicanus* female. In 1919 the number of hours during the same period with temperatures above 71° F. (21.7° C.) was 640, which would make possible an average of 8 egg masses per female. It will thus be seen that the potential capacity of *M. mexicanus* to increase itself was 2.4 times as great in 1919 as in 1918. As further evidence that the more favorable temperatures for oviposition were taken advantage of, it should be stated that while *M. mexicanus* was not unusually abundant in 1919, yet in 1920 it suddenly became more numerous than it had been for years.

It should not be understood from the foregoing discussion that temperature during the egg-laying period is the one deciding factor in grasshopper abundance. Parasites and disease, moisture conditions, and other factors all play their part, but the potentiality for increase is to a very large extent determined by the number of eggs deposited, which in turn, as has been shown, is greatly influenced by temperature during the egg-laying season.

In this connection the writer has often sought for an explanation of the fact that out of a total of about 100 species of grasshoppers found in Montana, only a few have ever become abundant enough to be of local economic importance, and only two species—*M. mexicanus* and *C. pellucida*—have ever increased to such numbers as to warrant extensive control campaigns. These two species sometimes increase to enormous numbers, while in exactly the same environment a score of

other species are found represented by only a few scattered individuals. A possible answer that has suggested itself from the present experiment is that the less abundant species are fixed in their capacity for egg laying, their ovaries being able to mature only a small number of egg pods under the most favorable conditions, while in the more destructive species the ovaries have become so specialized that egg production continues throughout adult life, whenever temperature conditions are favorable. Thus if one species was capable of laying only 2 egg pods per season it would probably be able to deposit its entire quota regardless of whether the summer was above or below normal in temperature, and would therefore remain at about the same level from year to year. A species capable of laying 20 egg pods per season might experience only enough hours of favorable temperatures to deposit 2 egg masses during a cool summer, while during a very warm year 20 egg pods might be deposited, thus allowing for great yearly fluctuations in numbers.

With this in mind 10 pairs of each of 4 economic species and an equal number of non-economic forms were collected in the field in August and held in cages at room temperature. The highest number of egg pods obtained from any one female was as follows:

Economic species		Non-economic species	
M. mexicanus	15	*Mestobregma kiowa*	1
C. pellucida	9	*Philbostroma quadrimaculatum*	2
Melanoplus bivittatus	4	*Amphitornus coloradus*	1
Melanoplus femur-rubrum	4	*Metator pardalinus*	1

A second experiment with the same end in view was conducted with grasshoppers collected from the field in late September. Pairs were not isolated as in the first experiment, and the results are therefore given as average egg pods per female rather than highest number of egg pods per female. The results were as follows:

Economic species		Non-economic species	
M. mexicanus	5.0	*Melanoplus gladstoni*	2.7
C. pellucida	4.5	*Melanoplus infantilis*	2.1
M. packardi	4.0	*P. quadrimaculatum*	.8
M. bivittatus	3.6	*Ageneotettix deorum*	.6

It should be stated that while *M. gladstoni* and *M. infantilis* are classed as non-economic species they are among the more common grasshoppers in Montana and are generally much more abundant than *P. quadrimaculatum* and *A. deorum*.

While these experiments were too limited in extent and started too late in the season to warrant making a definite statement in regard to the potential egg-laying capacity of the various species used, yet they do lend support to the suggestion made above that species of economic importance are able to occasionally increase to vast numbers largely because of their greater capacity for egg laying during periods of unusually favorable temperature conditions.

EFFECT OF TEMPERATURE UPON NUMBER OF NYMPHAL INSTARS

In connection with rearing a large number of individuals of *M. mexicanus* at constant temperatures, it was found that when reared at 22° and 27° C. there were always 6 instars, while at 32° and 37° C. there were only 5. At the higher temperatures the second and third instars ordinarily gone through are merged into one.

At alternating temperatures of 32° C. for 8 hours daily and 12° C. for 16 hours daily there were 6 instars, while at 37° C. for 8 hours and at 12° C. for 16 hours there were only 5 instars.

C. pellucida passed through 5 instars at all the temperatures at which it was reared—27°, 32°, and 37° C.

EFFECT OF TEMPERATURE UPON COLOR

The temperature at which *M. mexicanus* and *C. pellucida* are reared has a marked effect upon their color, high temperatures resulting in light-colored specimens while low temperatures result in very dark-colored individuals. The difference is especially striking in *M. mexicanus*. In adults reared at 37° C. the dark markings are much reduced, sometimes disap-

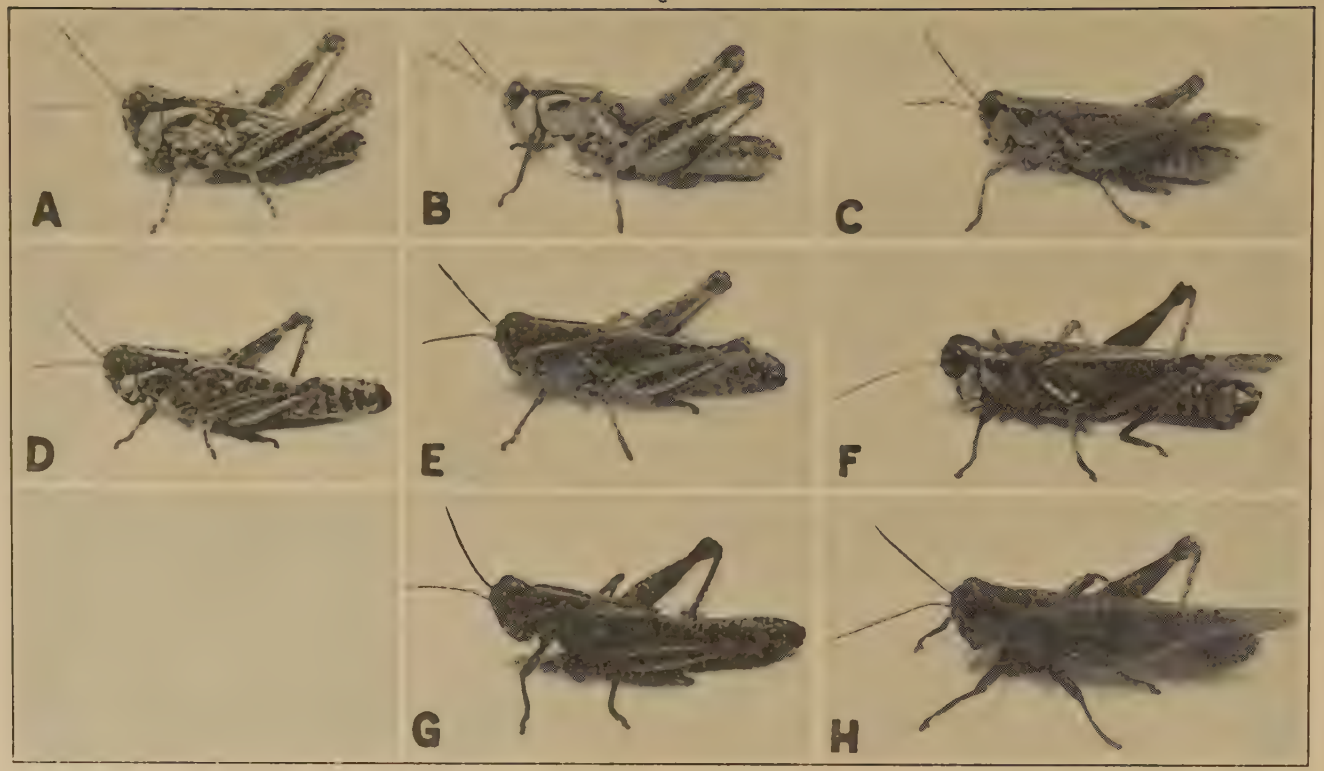

Figure 22.—Effect of temperature upon the color of **M. mexicanus.** Specimens A, B, and C were reared at a constant temperature of 37° C.; D, E, and F at a constant temperature of 32° C.; G and H at a constant temperature of 27° C.

pearing entirely on the femur and sides of the head. A portion of the black area behind the eyes and along the sides of the prothorax always remains and contrasts strikingly with the ground color, which varies from pale yellow to bright orange.

In adults of the same species reared at lower temperatures, the dark areas become progressively enlarged at 32° and 27° C. and at 22° C. the entire insect is uniformly dark brown or almost black.

Differences in color due to temperature are shown in Figure 22 but are not as marked as in the living insect.

INFLUENCE OF MOISTURE UPON EGGS

EFFECT OF SOIL MOISTURE UPON TIME NECESSARY TO HATCH AND PERCENTAGE OF EGGS HATCHED

The first experiment to determine the effect of moisture upon grasshopper eggs was conducted as follows: Eggs of *C. pellucida* were collected from moist soil in the field and taken to a greenhouse. Lots of 1000 eggs were counted out and placed at a depth of 2 inches in fairly dry soil in ordinary flower pots. To one series of pots no water was added; a second series received just enough water each day to keep the soil moist but not wet (150 to 250 cc. per pot); a third series received enough water each day to keep the soil thoroughly soaked (500 to 1000 cc. per pot). Temperature in the greenhouse varied from 90° F. during the warmest part of the day to 60° F. at night. Hatching began on the tenth day after the eggs were taken into the greenhouse. The number of grasshoppers hatched each day and the total number hatched from each series of moisture conditions, are shown in Table 39.

Hatching started first in the dry soil and was progressively slower in the moist and wet soils. In the moist soil 91.5 per cent of all the eggs hatched, while in the dry soil the percentage of hatch was reduced to 69.5, and in the wet soil to 72.6.

TABLE 39.—Effect of soil moisture upon time necessary to hatch, and percentage hatched in eggs of C. pellucida. Eggs taken from field and held in lots of 1000 in dry, moist, and wet soil.

Day	Number of eggs hatched each day in—		
	Dry soil	Moist soil	Wet soil
10	210	.....	.....
11	226	1	3
12	90	58	62
13	45	88	76
14	40	108	96
15	23	271	202
16	20	291	208
17	36	39	36
18	4	20	20
19	0	1	1
20	0	0	0
21	0	11	8
22	1	7	8
23	.....	20	0
24	.....	.....	4
25	.....	.....	0
26	.....	.....	1
27	.....	.....	1
Total	695	915	726

EFFECT OF SUBMERGING EGGS IN WATER

Eggs collected in the field at the same time as those in the foregoing experiment were divided into four lots of 1000 each, placed in cheese-cloth bags, and on May 27 were submerged in a tub of water which was placed beneath the greenhouse bench. On July 15 one lot was removed and the eggs placed in fairly dry soil. Hatching began in 15 days. A second lot was taken out on August 15 and started to hatch in 17 days; a third lot was taken out on September 15 and hatching began in 20 days; the fourth and last lot was allowed to remain in the water until January 15, and when taken out the eggs were decayed and never hatched. No accurate record was made of the number of eggs hatching per day or the percentage of eggs hatched. From general observation, however, the estimated percentage of eggs hatched was approximately as follows: Lot 1, submerged 49 days, 50 per cent; Lot 2, submerged 80 days, 35 per cent; Lot 3, submerged 110 days, 25 per cent.

This experiment indicates that grasshopper eggs in flooded areas, even though submerged for weeks, would not be entirely destroyed but would hatch at a later date when the water receded. Unbroken egg pods within their protective covering,

held under water at a fairly low temperature, would probably retain their viability to a greater extent than did the individual eggs submerged in water at the greenhouse temperatures.

EFFECT OF RELATIVE HUMIDITY UPON THE TIME NECESSARY TO HATCH AND THE PERCENTAGE OF EGGS HATCHED AT ROOM TEMPERATURE

The effect of relative humidity upon the time necessary to hatch and the percentage of eggs hatched was determined by holding lots of 100 eggs of both *M. mexicanus* and *C. pellucida* at room temperature (23°-25° C.) and constant relative humidities of 10, 18, 41, 70, and 97 per cent. These humidities were obtained by passing a current of air from a compressed air tank through sulphuric acid, saturated solutions of lithium chloride, copper nitrate, sodium chloride, and distilled water in the order named. Glass cylinders containing grasshopper eggs were introduced into the air line behind the solution, giving the desired humidity. Active humidities were checked from time to time by inserting a glass cylinder containing small wet and dry bulb thermometers into the air line in place of the cylinder containing eggs. Half of the eggs used had previously been kept in damp sand for several months at 2° to 7° C., after being collected in the field, and half were kept in dry sand for several weeks at the same temperature. The results are shown in Table 40.

Eggs of both species previously held in damp sand hatched first at low humidities, while eggs previously held in dry sand hatched first at high humidities. *C. pellucida* eggs from damp sand held at relative humidities of 10 and 18 per cent gave the largest percentage of eggs hatched. In the other three lots the highest percentages of eggs hatched were in every case obtained at 70 per cent relative humidity. At 97 per cent relative humidity some of the eggs always molded, while at 18 and 10 per cent relative humidity many of the eggs from dry sand shrivelled and collapsed. This was especially true of *M. mexicanus* eggs, which are thinner shelled than those of *C. pellucida*.

TABLE 40.—Effect of relative humidity upon time necessary to hatch and percentage of eggs hatched at room temperature (23°-25° C.) in field collected eggs of **M. mexicanus** and **C. pellucida.**

% relative humidity	Number of eggs hatched each day														Total number hatched
	Day 8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
							100 **C. pelludica** eggs from damp sand								
97	....	....	....	....	....	9	8	3	....	....	....	....	....	....	....	20
70	....	....	....	4	3	33	3	2	....	....	....	....	....	....	....	45
41	....	....	....	11	5	32	1	1	....	....	....	....	....	....	....	50
18	....	....	....	5	2	60	3	0	0	0	1	1	....	....	....	72
10	....	....	....	5	8	54	3	0	0	0	0	1	....	....	....	71
							100 **C. pellucida** eggs from dry sand								
97	....	....	....	....	....	....	5	3	5	10	1	0	1	....	....	25
70	....	....	....	....	....	....	3	1	0	34	0	0	0	1	....	39
41	....	....	....	....	....	....	10	9	9	0	1	0	1	....	....	30
18	....	....	....	....	....	....	....	....	8	8	....	....	....	....	....	16
10	....	....	....	....	....	....	....	....	1	4	....	....	....	....	....	5
							100 **M. mexicanus** eggs from damp sand								
97	....	....	....	14	3	8	6	0	0	10	8	....	....	....	....	49
70	....	17	12	11	4	1	1	1	14	....	....	....	....	....	....	61
41	....	7	4	7	3	1	4	0	0	6	5	....	....	....	....	35
18	18	16	2	2	0	1	....	....	....	....	....	....	....	....	....	39
10	....	3	2	0	0	0	0	1	....	....	....	....	....	....	....	6
							100 **M. mexicanus** eggs from dry sand								
97	....	....	....	....	....	2	0	0	3	0	4	5	10	8	2	34
70	....	....	....	....	....	....	....	10	10	0	0	5	1	2	5	33
41	....	....	....	....	....	....	....	....	9	3	0	0	0	0	1	13
18	....	....	....	....	....	....	....	....	....	....	0	0	0	0	....	0
10	....	....	....	....	....	....	....	....	....	....	0	0	0	0	....	0

EFFECT OF RELATIVE HUMIDITY UPON PERCENTAGE OF EGGS HATCHED AT CONSTANT TEMPERATURES

In this experiment field-collected eggs of *M. mexicanus* were kept at constant temperatures and constant relative humidities. Stoppered glass jars containing solutions of sulphuric acid and water of known specific gravity provided constant relative humidities ranging by 10 per cent intervals from 10 to 100 per cent. Four sets of jars were prepared, one set being kept at each of the following constant temperatures, 22°, 27°, 32°, and 37° C. Lots of 100 *M. mexicanus* eggs were placed in small glass cylinders closed at each end with gauze, and one lot was suspended in the air above the liquid in each of the jars. The percentage of eggs hatching at each temperature and relative humidity is shown in Table 41.

Table 41

Percentage of Melanoplus atlanis eggs hatching at different constant temperatures and constant Relative Humidities.

Per Cent R. H.	22°C.	27°C.	32°C.	37°C
100	44 per cent	24 per cent	36 per cent	24 per cent
90	48	72	52	48
80	54	58	34	28
70	32	36	24	4
60	24	20	2	0
50	20	6	0	0
40	12	6	0	0
30	4	0	0	0
20	0	0	0	0
10	0	0	0	0

At 22° C. the highest percentage of eggs hatched at 80 per cent relative humidity while at 27°, 32°, and 37° C. the optimum was at 90 per cent. The higher the temperature the narrower was the range of relative humidity within which hatching took place. Thus at 37° C. no hatching occurred except from 70 to 100 per cent, while at 22° C. hatching took place throughout the range from 30 to 100 per cent. An examination of the data shown in the table shows a rather definite zone of temperature and relative humidity where conditions for hatching are at the optimum, and somewhat resembles in this respect Pierce's graph (12) showing the relation of temperature and humidity to cotton boll weevil activity.

EFFECT OF RELATIVE HUMIDITY UPON TIME NECESSARY TO HATCH AT CONSTANT TEMPERATURE

Overwintered field-collected eggs of *C. pellucida,* taken from fairly damp soil and held in damp sand at 2° to 7° C. until used, were counted into lots of 100 and suspended over sulphuric acid and water solutions arranged to maintain relative humidities from 10 to 100 per cent at 10 per cent intervals. The humidity jars were maintained at a constant temperature of 27° C. and close watch was kept for the first sign of general hatching. The time necessary to hatch is shown graphically in Figure 23.

Eggs at 10 and 20 per cent relative humidity never hatched. At 30 per cent they started to hatch in 13 days; at 40 per cent in 12 days; at 50 per cent in 11 days, and at 60, 70, 80, 90, and 100 per cent in 10 days. This is in reverse order to the hatching of similar eggs held at room temperature (23°-25° C.), in which case hatching occurred first at the lower relative humidities and last at the higher relative humidities. The only explanation suggested is that at the higher temperature of 27° C. the moisture content of the eggs held at low relative humidities was reduced more rapidly than at room temperatures, and resulted in such a low moisture content that hatching was retarded to a greater extent than in eggs with higher moisture content. In support of this statement it was noticed that eggs held at 10 per cent relative humidity at 27° C. for 10 days were more shrunken in appearance than those held for the same

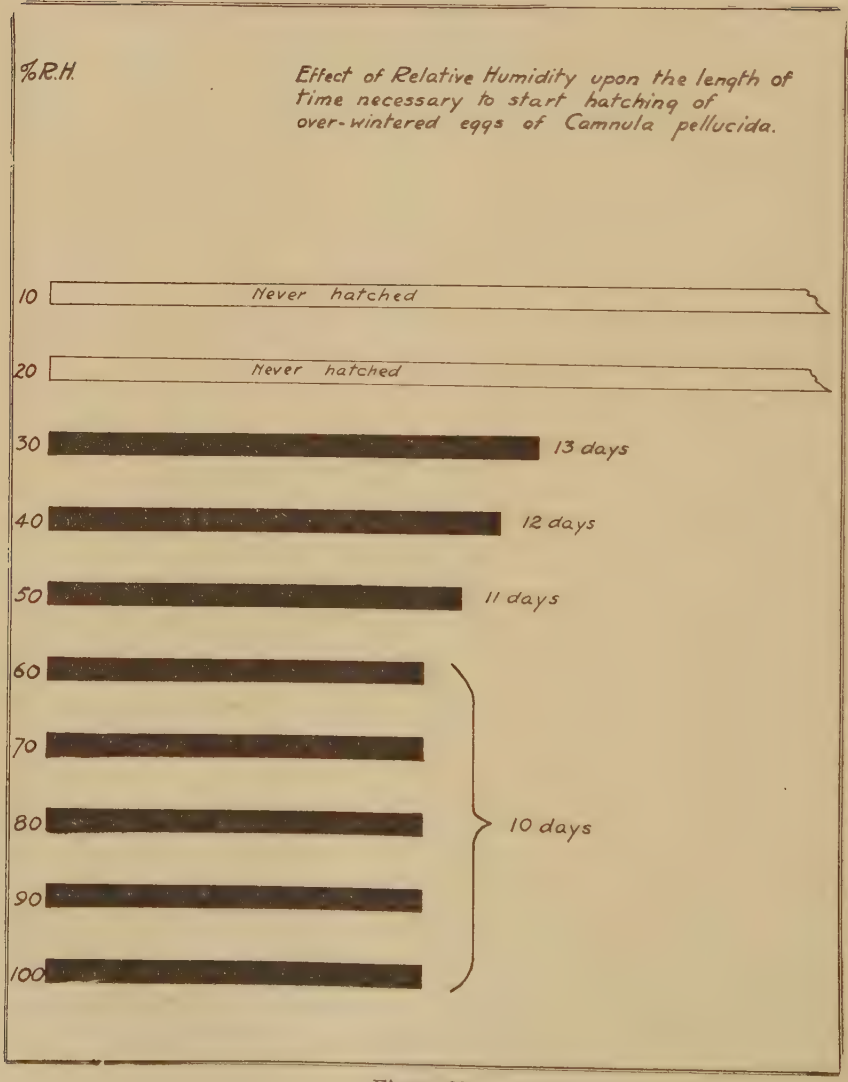

Figure 23

length of time and relative humidity at room temperature. Experiments to be reported under the next heading also indicate that at 27° and 37° C. hatching was retarded by a lowering of the moisture content of the eggs.

EFFECT OF RELATIVE HUMIDITY UPON MOISTURE CONTENT OF EGGS

In this experiment it was desired to find out how much of their original weight grasshopper eggs lost at different constant temperatures and relative humidities and how this loss in weight affected their viability. Constant relative humidities ranging by 10-degree intervals from 10 to 100 per cent were obtained by using solutions of sulphuric acid and water of the proper specific gravity. One set of relative humidity jars was kept at a constant temperature of 27° C. and another at 37° C. *C. pellucida* eggs kept previously in damp sand at 2° to 7° C. were counted into lots of 100 and carefully weighed. One lot was suspended in the air above the liquid in each of the relative humidity jars. Daily weighings were made of all lots to determine their loss of weight for each 24-hour period. As soon as hatching was noticed in any lot the remaining eggs in that lot were removed from the humidity jars and placed in damp sand at 32° C., where they were held until hatching was completed. The few eggs which hatched in the humidity jars were also included in the figures given in the column headed "Percentage hatched in damp sand at 32° C." Lots of eggs which at the end of 16 days had shown no sign of hatching were also removed and placed in damp sand at 32° C. The daily weight of each lot of eggs, the percentage of its original weight lost during the time spent in the humidity jar, and the percentage of eggs that hatched when later placed in damp sand at 32° C. are shown in Table 42.

It is of interest to note that at the lower relative humidities, a few eggs hatched even after they had lost over 50 per cent of their original weight. When taken from the humidity jars all these eggs were shrivelled and collapsed to such an extent that it was not expected that any of them would survive. However, some of them when placed in damp sand at 32° C. regained their original plumpness and produced normal young grasshoppers. In the two lots which lost the largest percentage of their original weights, 66.4 and 68 per cent, none of the eggs survived. Percentage of eggs hatched in almost every instance increased as the percentage of original weight lost decreased.

TABLE 42.—Percentage of original weight lost by **C. pellucida** eggs held at constant temperatures and relative humidities and its effect on percentage hatched when eggs were removed and placed in damp sand at 32° C.

27° C.	Daily weights in milligrams of lots of 100 eggs																	% original weight lost	% hatched in damp sand at 32° C.
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17		
10% R. H.	648	583	555	524	493	466	443	419	396	377	358	343	328	313	296	284	*	56.2	10
20	651	599	572	547	521	498	472	455	434	414	396	379	359	348	330	315	*	51.6	15
30	660	612	588	566	546	522	502	490	462	443	427	412	†	*				37.6	8
40	652	608	587	572	555	537	620	501	484	466	452	†	*					30.7	18
50	684	652	634	619	601	568	547	525	504	484	†	*						29.2	39
60	661	630	618	598	582	569	547	530	513	†	*							22.4	41
70	691	666	655	645	632	615	602	586	568	545	†	*						21.1	60
80	668	647	637	623	617	608	597	584	570	551	†	*						17.5	69
90	645	624	622	615	613	606	598	591	582	563	†	*						12.7	72
100	653	644	640	634	634	625	620	614	608	†	*							9.0	74
37° C.																			
10% R. H.	687	611	580	545	505	482	459	432	407	384	361	342	317	302	298	260	*	62.	14
20	625	551	514	486	449	427	398	368	324	304	286	272	253	243	224	210	*	66.4	0
30	622	582	533	491	446	425	390	354	326	294	271	253	233	223	209	198	*	68.0	0
40	630	585	549	521	487	464	438	411	384	360	339	320	297	285	264	250	*	60.5	16
50	655	602	574	550	519	497	472	439	†	*								33.0	47
60	683	635	614	590	560	535	511	†	*									25.2	48
70	682	644	623	604	576	550	†	*										19.2	55
80	656	629	608	593	573	561	†	*										14.4	58
90	672	650	640	627	608	591	†	*										12.0	74
100	674	664	662	658	649	637	†	*										5.5	58

†—First hatching. *—Eggs removed and placed in damp sand at 32° C.

As was to be expected, eggs held at the same relative humidities lost weight more rapidly at 37° C. than at 27° C., and eggs held at the same temperature lost more weight at low relative humidities than at higher ones. An exception to the latter statement occurred in the series held at 37° C., eggs held at relative humidities of 20 and 30 per cent losing more weight than eggs held at 10 per cent. A possible explanation for this might be that the eggs were thinner shelled. This is indicated by the fact that the original weights of these two lots of eggs were the lowest of the 20 lots used in the experiment. The slight loss of weight in eggs held at 100 per cent relative humidity may have occurred during the time when the eggs were removed to the dry atmosphere of the laboratory for their daily weighing.

A similar experiment was conducted with eggs of both *M. mexicanus* and *C. pellucida* to obtain their relative reduction in moisture content when held at the same temperature and relative humidity. One hundred eggs of each species, previously held in damp sand at 2° to 7° C., were weighed and placed in an open container which was kept at a constant temperature of 27° C., the relative humidity in the temperature cabinet ranging from 20 to 25 per cent. The eggs were weighed each day for 5 days and were then removed and placed in damp sand at 32° C. to determine the percentage of eggs that would hatch. The results are shown in Table 43.

TABLE 43.—Comparison of percentage of original weight lost by **M. mexicanus** and **C. pellucida** eggs in 5 days at 27° C. and their effects on percentage of eggs hatched when eggs were removed and placed in damp sand at 32° C.

	Daily weights in milligrams of 100 eggs at 27° C. and 20% to 25% relative humidity					Percentage of original weight lost	Percentage hatched later in damp sand at 32° C.
	Day 1	2	3	4	5		
M. mexicanus	528	395	312	285	258	51.1	34
C. pellucida	663	599	542	506	470	29.1	80

At the end of the 5-day period eggs of both species were all more or less shrunken, *M. mexicanus* eggs having lost 51.1 per cent of their original weight, and *C. pellucida* 29.1 per cent. After ten days in damp sand at 32° C., 97 eggs of *C. pellucida* and 42 eggs of *M. mexicanus* had regained their original plumpness and weight, the others remaining shrunken and collapsed.

Eventually 80 per cent of the original number of *C. pellucida* eggs hatched and 34 per cent of *M. mexicanus*.

The results of the foregoing experiments offer an explanation of how grasshopper eggs are killed by the well-known and simple method of disking, or otherwise working the soil in which they are found. Such cultivation results in bringing to the surface and in breaking open some of the egg pods, thus exposing the eggs to higher temperature and lower humidities than would be found in undisturbed ground. As a result, many of the eggs shrivel and lose weight beyond the point where moisture coming at a later date can restore them to normal condition. From the experimental evidence, eggs of *M. mexicanus* should be more susceptible to this method of control than eggs of *C. pellucida*.

EFFECT OF MOISTURE UPON UNDERCOOLING AND FREEZING POINT

It has been pointed out earlier in this paper (page 38) that the undercooling and freezing points of *M. mexicanus* and *C. pellucida* eggs which had been previously kept in moist sand at 22° C. were higher than for eggs which were partially dried out by storage in dry sand at the same temperature. Eggs of *M. mexicanus* showed an average difference of 1.7° C. in both undercooling and freezing points, while with *C. pellucida* eggs there was a difference of 1.1° C. in the freezing points and 1.4° C. in the undercooling points. Grasshopper eggs brought to the surface by cultivation or exposed by soil blowing are subject to lower temperatures than eggs deeper in the ground; but their cold resistance, judging from the foregoing experimental evidence, is slightly increased by their lower moisture content, which results from their location in the drier surface soil.

EFFECT OF MOISTURE ON DEATH POINT OF EGGS AT HIGH TEMPERATURE

In connection with experiments undertaken to determine what high temperatures were necessary to kill grasshopper eggs (page 42), it was found that at temperatures sufficiently high to materially reduce the viability of the eggs the reduction was greater in eggs previously kept in moist sand than in eggs from dry sand.

In the case of *C. pellucida* eggs, 20 per cent of those from damp sand remained viable after an exposure of 10 minutes at

60° C. as compared with 52 per cent after the same treatment of eggs from dry sand. After one hour at 50° C., 26.5 per cent of the eggs from damp sand were viable as compared with 52 per cent from dry sand.

M. mexicanus eggs showed the same tendency, 8 per cent of those from dry sand remaining viable after a 10-minute exposure at 60° C. and 16 per cent after one hour at 50° C. Eggs from dry sand subjected to the same exposures were respectively 12 and 28 per cent viable.

Grasshopper eggs in dry soil close to the surface of the ground have a lower moisture content than eggs deeper in the soil, and are therefore better adapted to withstand the higher temperatures to which they are exposed.

INFLUENCE OF MOISTURE UPON NYMPHS AND ADULTS

GENERAL DISCUSSION

Determining the influence of moisture upon adult and nymphal grasshoppers is a much more difficult problem than studying the effects of temperatures. Maintaining constant relative humidities at which grasshoppers could be reared in numbers proved to be a problem which was never satisfactorily solved. A battery of Carrier Air Conditioning Cabinets would have offered suitable conditions but the cost was far in excess of the funds available. Relative humidities obtained by the use of a solution of sulphuric acid and water in closed chambers did not prove satisfactory, a much higher mortality occurring under such conditions than where a greater circulation of air was possible. Passing a current of air through saturated solutions of chemicals proved to be the best method tried, but the difficulty met in keeping the system operating uniformly for a period long enough to carry grasshoppers from the egg to the adult stage was so great that only a limited number of rearings were obtained.

EFFECT OF RELATIVE HUMIDITY UPON RATE OF DEVELOPMENT

A few specimens of *M. mexicanus* and *C. pellucida* were carried throughout the nymphal stage at a constant temperature of 32° C. and at relative humidities of approximately 18 and 70 per cent. In 16 specimens of *M. mexicanus* reared at

70 per cent relative humidity, the length of the nymphal period varied from 23 to 34 days and averaged 26.6 days, while 12 specimens reared at 18 per cent relative humidity varied from 24 to 35 days and averaged 27.2 days. In 9 specimens of *C. pellucida* reared at 70 per cent relative humidity, the length of the nymphal period varied from 21 to 32 days and averaged 26.1 days, while 12 specimens reared at 18 per cent relative humidity varied from 22 to 30 days and averaged 25.3 days. These slight differences do not indicate that relative humidity has any marked effect on the rate of nymphal development. However, the number of specimens that it was possible to rear was so small that no definite conclusions are warranted.

TIME NECESSARY TO KILL GRASSHOPPERS BY SUBMERGING IN WATER

Experiments conducted to determine the time required to kill grasshoppers by drowning showed that the temperature of the water in which they were submerged was a very important factor.

A number of coarsely screened vials, each containing 10 nymphs of *C. pellucida*, were immersed in water held in containers in constant temperature cabinets ranging from 0° to 37° C. One vial from each temperature was removed every hour until a point was reached at which none of the 10 nymphs recovered after being removed from the water and placed on filter paper in a warm room. The time required to kill all 10 nymphs was as follows: 3 hours at 37° C., 7 hours at 32° C., 13 hours at 27° C., 19 hours at 22° C., 20 hours at 19° C., 36 hours at 17° C., 60 hours at 12° C., 72 hours at 7° C., and 84 hours at 0°-1° C. These results are shown graphically in Figure 24.

This indicates that flooding infested fields with irrigation water during very warm weather would be much more effective in killing grasshoppers than during cold weather. It also explains why heavy rains of short duration during cool weather fail to materially decrease the grasshopper population even though many grasshoppers are under water for hours. Grasshoppers are frequently found embedded in the mud in depressions where rain water has stood for a few hours and if removed they will, in many instances, become entirely normal. The tem-

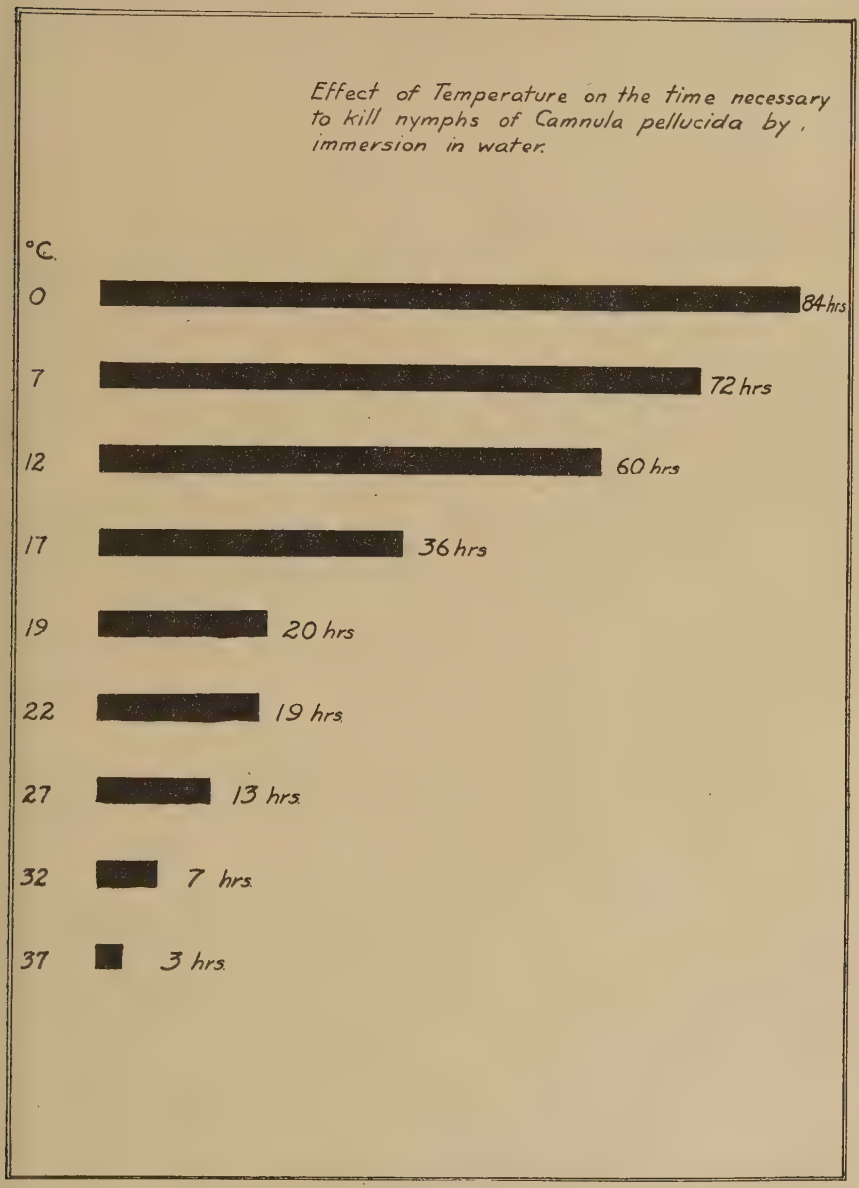
Effect of Temperature on the time necessary to kill nymphs of Camnula pellucida by immersion in water.
°C.
0
84 hrs
7
72 hrs
12
60 hrs
17
36 hrs
19
20 hrs
22
19 hrs
27
13 hrs
32
7 hrs
37
3 hrs

Figure 24

perature factor may also explain why a grasshopper impaled on a fish hook lives longer in the cold water of a mountain lake than in the warmer water of shallow streams and ponds at lower altitudes.

INDIRECT EFFECT OF MOISTURE BY MAKING CONDITIONS FAVORABLE FOR FUNGOUS AND BACTERIAL DISEASES

Excessive moisture, because it provides ideal conditions for the development of fungous and bacterial diseases of grasshoppers, is indirectly one of the most important, if not the most important, natural checks upon grasshopper abundance. During periods of wet, cloudy weather when the relative humidity is continuously close to the saturation point for days at a time, grasshoppers may suddenly start dying by the millions. Warm dry weather generally checks such epidemics but sometimes not before a very high percentage of the grasshopper population has been wiped out. While many reports of the dying of grasshoppers during or following wet weather can be found in entomological literature, few of them give any record of the prevailing moisture and temperature conditions. Aughey (1) in his daily record of grasshopper conditions at Lincoln, Nebraska, in 1877, gives the nearest approach to exact meteorological data. During 1876 great swarms of the Rocky Mountain locust *(M. spretus)* had laid enormous numbers of eggs in the vicinity of Lincoln. These started to hatch on April 14 of the following spring, young grasshoppers appearing in such enormous numbers that it was expected all crops would be destroyed. Continuous cold weather from April 16 to April 20 checked the hatching temporarily and many of those already hatched started to die. Later, whenever there was a warm day, enormous numbers would hatch from the ground only to die during the wet weather that followed. While no record of the exact amount of rainfall is given, Aughey in his diary reports heavy rains on May 5, 6, 9, 10, 11, 12, 14, 16, 17, 18, 19, and 20. Nearly every entry during this period contains such remarks as "found millions of dead locusts," "found great numbers of dead locusts and many dying," "at one place found dead locusts 3 inches thick on the ground." On May 21 the entry was as follows: "Temperature 2 p. m. 79° F. Found many dead and dying

locusts today. Weather sultry. Locusts seem to die off as fast in warm, wet weather as in cold, wet weather." As a result of the ravages of disease only a very small percentage of the grasshoppers that hatched reached maturity, comparatively little crop damage took place, and a 4-year period of enormous grasshopper abundance was brought to a close.

Doctor S. B. Fracker kindly supplied information concerning the effect of wet weather upon *C. pellucida* in Wisconsin: "The most notable reduction in grasshopper population on account of inclement weather which has occurred in Wisconsin was in 1924. Mr. Chambers made a survey of Marinette and Florence Counties about June 15 and found grasshoppers hatching in large numbers. Arrangements were made with the town boards for securing sufficient poison and surveys made as to the localities in which damage might be expected. About July 10 he returned and found that the hoppers had practically disappeared." No poison was used and wet weather was generally considered to have caused the death of the young hoppers. The weather record for Brule Island, in the infested area, is as follows:

	June			July									
	28	29	30	1	2	3	4	5	6	7	8	9	10
Precip.	.42	.60	.08	.08	.02	0	.11	.15	0	.09	.75	.10	0
Max. temp.	72	72	63	86	70	75	78	81	80	73	74	74	81
Min. temp.	51	50	47	50	44	43	45	56	51	50	56	62	54

In 1923 the start of a disease attack upon *C. pellucida* was personally witnessed near Duluth, Minnesota. A large colony of this species was under daily observation and up to July 2 had appeared perfectly normal. On July 3 a dense fog rolled in from Lake Superior and from then until July 7 the relative humidity, according to hygrograph records, was seldom below 98 per cent, the entire period being rainy and such a dense fog prevailing as to make necessary the use of automobile headlights in midday. Temperature records were as follows:

	July							
	2	3	4	5	6	7	8	9
Maximum temp.	73	73	72	58	57	61	80	87
Minimum temp.	52	56	52	49	49	52	51	66

After three days of this weather it was noticed that a few grasshoppers were dying of what appeared to be a bacterial disease and on the fourth day their dead bodies could be seen attached in large numbers to weeds and grass upon which they climbed in the last stages of the disease. On the afternoon of the fifth day the air cleared and the several days of bright sunshine which followed completely checked the disease which threatened the entire local grasshopper population had the wet weather continued much longer.

Another example of the effect of continued wet weather upon *C. pellucida* was personally observed in Montana in 1925. Warm weather during the last few days in May hatched large numbers of young grasshoppers in the vicinity of Springhill, 18 miles north of Bozeman, and farmers were greatly concerned over the safety of their crops and called for advice on control measures. The first half of June was almost continuously cloudy and wet, and as a result, the young grasshoppers died in such numbers that poisoning was not necessary. The nearest weather records available are those at Bozeman where the rainfall as a rule is slightly less than at Springhill. They are as follows:

	June																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Precip.	.08	.01	.11	.07	.33	.07	0	.07	.01	.65	.05	.03	.03	.01	.01	.38	.02	0
Max. temp.	55	58	57	52	45	61	59	64	70	60	57	56	62	66	63	67	71	77
Min. temp.	39	38	37	37	35	35	37	37	47	33	31	37	36	39	49	42	44	46

Additional instances of grasshoppers dying during or following periods of wet weather could be cited but daily weather records are not available to show the exact conditions under which disease conditions were prevalent. From the history of the instances in which a record of meteorological conditions was available, it is evident that periods of continuously cloudy or wet weather lasting from 3 to 5 days bring about conditions which are very favorable to the fungous and bacterial diseases to which grasshoppers are susceptible. Continuous high relative humidity seems to be a more important factor than either total rainfall or temperature, epidemics of disease having occurred at both comparatively low and high mean temperatures and during rather light daily precipitations.

The enormous and rapid destruction of grasshoppers that has actually been witnessed in the few cases reported, coupled with the generally accepted fact that periods of great grasshopper abundance are usually terminated by a year or two of high rainfall, leads to the conclusion that excessive moisture acting as a promoter of fungous and bacterial diseases is one of the greatest natural checks with which grasshoppers must contend.

INDIRECT EFFECT OF MOISTURE THROUGH THE FOOD SUPPLY

An abundance or a lack of soil moisture may affect grasshoppers indirectly through their food. This relation was first suggested by observation of a colony of *M. femur-rubrum* nymphs in an isolated grassy area among the sand dunes near St. Paul, Minnesota. By the time the nymphs were half grown the grass was becoming very dry, but, being surrounded by sand, most of the colony remained there and many came through to maturity on the parched grass. It was noticed that they were unusually long winged, and, as a matter of curiosity, 25 males were collected from the dry area and compared with a similar number of males collected in succulent meadow grass about a quarter of a mile from the sand dune area. In the sand dune series the average distance from the end of the abdomen to the tip of the wing was 0.17 of an inch, while in the meadow series it was only 0.10 of an inch.

In rearing *M. mexicanus* it was found that specimens reared exclusively on green succulent food such as *Tradescantia* were smaller and had relatively shorter wings than when a mixture of green food and dried alfalfa leaves was used, or when dried alfalfa was used alone in the later instars.

In one series of 10 *M. mexicanus* males reared at 32° C. and fed after the first molt entirely on dried alfalfa, the average distance from the end of the abdomen to the tip of the wing was 0.30 of an inch, while in 12 males reared at the same temperature and fed green food only the average distance was 0.15 of an inch.

In Montana it has been noted by field observations and from the studies of systematic workers that during outbreaks of *M. mexicanus,* which usually occur during dry weather, there

is a tendency toward greater size and relatively longer wings. No detailed measurements of large series of specimens collected during wet and dry years have as yet been made, but it is perhaps significant that the longest-winged *M. mexicanus* male in the large series of this species in the Montana Experiment Station collection was taken in parched grass during an outbreak in western Montana in 1917. In this specimen the wings extend 0.45 of an inch beyond the tip of the abdomen, or three times as far as in the average specimen reared on green food in the laboratory.

Similar differences have been noted in *C. pellucida* and it was called to my attention by E. R. Buckel, entomologist in charge for British Columbia, that specimens of this species collected in the humid areas along the Pacific Coast are decidedly smaller than specimens obtained on the high rolling hills of central British Columbia where native grasses are less succulent and frequently are suffering for moisture before *C. pellucida* has completed its nymphal development.

Uvarov (20), Plotnikov (13), Johnson (8), and others have rather conclusively shown that certain European and African grasshoppers which ordinarily occur in small numbers as scattered non-migratory individuals may, under favorable conditions, develop a migratory phase which not only increases to enormous numbers but is so different in appearance as to have been looked upon for years by systematic workers as a distinct species. The chief differences between the solitary and the migratory phases are in color, wing development, relative proportions of the pronotum, and in habits of migration.

In the United States several workers are inclined to the belief that the Rocky Mountain locust *(M. spretus* Walsh), now supposed to be extinct, was merely a migratory phase of *M. mexicanus*. Hebard, one of the foremost systematic workers in Orthoptera, after studying a series of 1645 specimens of *M. mexicanus* collected in Montana during the period from 1900 to 1927, makes the following statement (6) :

"In a few of the series here recorded the size average is large and the length of the organs of flight above average. Only in occasional specimens from such series taken in 1917, however, is approach toward *spretus* (Walsh) shown, and in these there

is little indication of a strangulate pronotum and other subtle features which give a distinctive appearance to series typical of that insect. We believe it wiser to consider these specimens representative of *mexicanus* showing decided divergence toward *spretus* in size and wing length, particularly as they were taken with large series to individually varying degrees more typical of the former. It is quite possible, as we have already stated, that *spretus* is not a distinct species but a migratory phase of *mexicanus*. Even more striking differences are shown between other species of grasshoppers and the migratory phases they are known to develop."

Should it be proven that *spretus* is merely a migratory phase of *mexicanus*, the moisture factor, acting through the food supply, is here suggested as one of the reasons for bringing about such a remarkable change in the appearance and habits of this grasshopper. Let us look for a moment at the history of grasshopper outbreaks and the weather records at Fort Shaw, Montana. This old military outpost is located in the heart of what Riley (14) termed the "permanent breeding ground" of the Rocky Mountain locust *(M. spretus)*. From this general area, during the early pioneer days, originated enormous swarms of grasshoppers which at times migrated as far east as the Mississippi Valley, devastating localities in which they happened to land for rest and food. Riley (14) states: "At Fort Shaw, 1873, 1874, 1875 were locust years. In 1875 they were most destructive."

Weather records were begun at Fort Shaw in 1868. An examination of these shows that for 4 years previous to this series of bad grasshopper years the rainfall was considerably below normal for the months of May, June, and July, and, in fact, it was the driest period of years in the entire set of records. Starting with 1876 came a series of years in which the rainfall was close to or above normal, during which time *M. spretus* diminished very rapidly in numbers and finally disappeared entirely from Montana, the last available record being from Glendive in 1885. In 1917 there began another series of dry years and from then until 1922 the rainfall during May, June, and July was continually below normal but did not fall to the low level reached during the period from 1869 to 1875. See Figure 25.

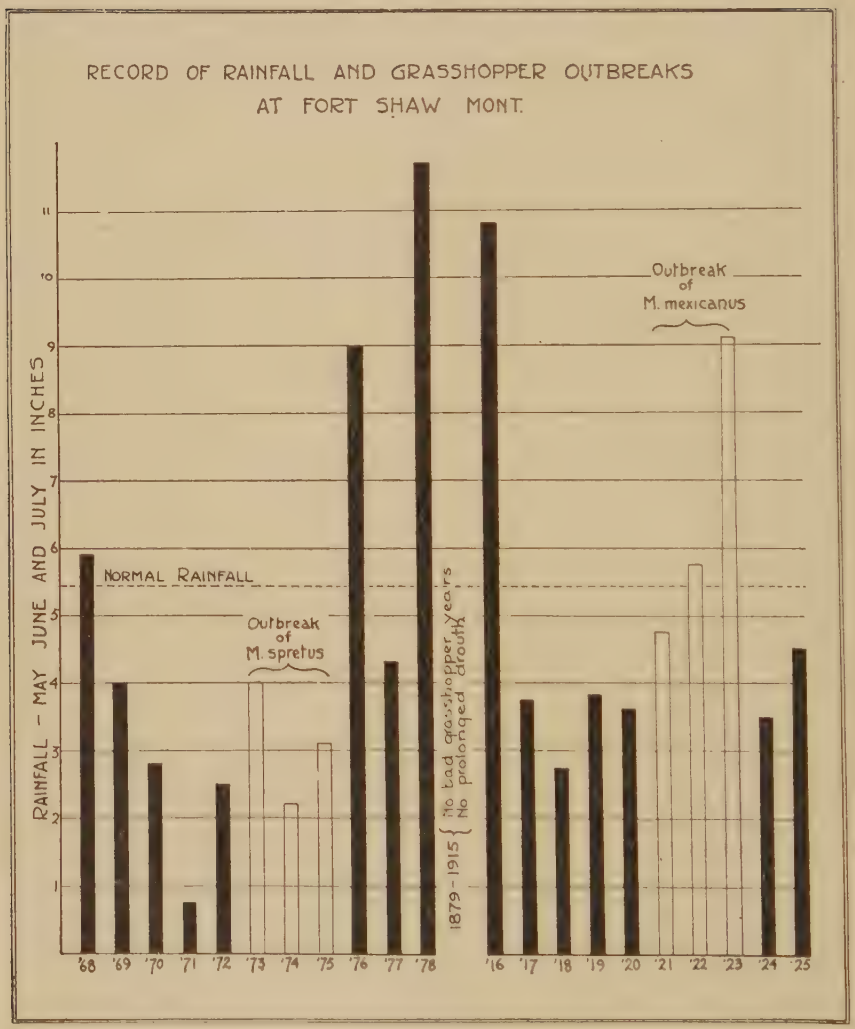
RECORD OF RAINFALL AND GRASSHOPPER OUTBREAKS
AT FORT SHAW MONT.
RAINFALL - MAY JUNE AND JULY IN INCHES
NORMAL RAINFALL
Outbreak of M. spretus
Outbreak of M. mexicanus
1879-1915 { No bad grasshopper years No prolonged drouth
'68 '69 '70 '71 '72 '73 '74 '75 '76 '77 '78
'16 '17 '18 '19 '20 '21 '22 '23 '24 '25

Figure 25

During this later dry period *M. mexicanus* increased very rapidly, and by 1920 had reached the point where a control campaign was necessary. Some idea of its abundance during this period can be gained from the number of acres which were treated with poisoned bran mash. In the county in which Fort Shaw is located the figures are as follows:

1920	4,000 acres
1921	13,900 acres
1922	50,000 acres
1923	51,000 acres
1924	8,000 acres
1925	None

During this outbreak it was noticed that *M. mexicanus* became more highly colored, was somewhat larger in size, and had relatively longer wings and stronger powers of flight than under normal conditions. Flights of swarms from one county to another were common, and Canadian Government officials called attention to the fact that swarms were flying from Montana into Alberta. In other words, *M. mexicanus* was closely approaching in appearance and habits *M. spretus* which, during a similar period of drought 50 years earlier, had devastated this same region, only to disappear with the return of normal rainfall. Had the last period of drought been as extreme as the earlier one, and had control operations not been so extensively practiced, it seems possible that this tendency might have developed to an even greater extent and that we should have had actual proof that *M. mexicanus* and *M. spretus* were one and the same species.

During periods of drought, grasshoppers hatching in May and early June generally have plenty of green succulent food during the early instars, but the grass frequently becomes dry and parched during the later stages of nymphal development. Periods of drought are also usually accompanied by high temperatures, especially of the soil surface, since vegetation is scant and provides less shade than when there is a luxuriant growth. Since in laboratory experiments more concentrated foods have had a tendency to produce larger and relatively longer-winged grasshoppers and high temperatures have produced more highly colored specimens, it is here suggested that similar conditions produced in nature by drought are very likely responsible for the changed appearance of *M. mexicanus* during exceptionally dry years. A tendency to longer-winged forms with increased powers of flight and a stimulated instinct for migration, seems a logical adaptation of the species to a climate in which prolonged periods of drought occasionally occur, since

it provides for an escape from ultimate starvation to areas where food is more abundant.

It is realized that there is not yet sufficient experimental evidence to warrant the assertion that *M. mexicanus* and *M. spretus* are identical, nor that the moisture content of food is the controlling factor in wing length. However, it has seemed worth while to indicate the possibility that such might be the case and to point out the desirability and importance of future work on this intensely interesting phase of the grasshopper problem.

SUMMARY

When eggs of *M. mexicanus* were placed at constant temperatures the day they were laid, the average length of the egg stage and the percentage of total development per day were as follows: 22° C.—147 days, 0.68 per cent; 27° C.—26 days, 3.84 per cent; 32° C.—32 days, 3.13 per cent; 37° C.—46 days, 2.17 per cent.

Eggs of *M. mexicanus* placed at 0° C. immediately after they were laid and later placed at constant high temperatures of 27°, 32°, and 37° C. developed more rapidly than when placed directly at these temperatures. Acceleration varied directly with the constant high temperature to which the eggs were returned, amounting to 136.7 per cent at 27° C., 357.5 per cent at 32° C., and 558 per cent at 37° C. Acceleration at all three temperatures increased as the length of the exposure to low temperature was increased until a period of 240 days was reached. Extending the exposure from 240 to 500 days resulted in only slightly increased acceleration.

Eggs of *M. mexicanus*, allowed partial development after being laid and then held at low temperatures for varying periods of time, showed an increase in rate of development when later returned to constant high temperatures. In partially developed eggs maximum acceleration was produced by an exposure of 60 days as compared with 240 to 300 days in undeveloped eggs. Exposure to 0° C. resulted in greater acceleration than at 8° C.

When eggs of *M. mexicanus* and *C. pellucida* were kept for 16 hours each day at 22° C. and 8 hours at higher temperatures of 27°, 32°, and 37° C., both species showed an increase over the rate of development at constant temperatures, the average acceleration for *M. mexicanus* being 38.6 per cent and for *C. pellucida,* 30.5 per cent. When eggs were kept for 16 hours daily at 12° C. and 8 hours at 27°, 32°, and 37° C., a still greater acceleration was obtained. Reciprocal growth curves for alternating temperatures, although showing a higher rate of development, are of the same type as those for constant temperatures.

Retardation in development of *M. mexicanus* eggs at high temperatures and accelerated development following exposures to low temperatures are beneficial to this species, since they prevent eggs laid early in the summer from hatching in the fall when growth could not be completed and bring about complete hatching during a few days in the spring of all eggs laid over a period of several months during the previous summer and fall.

Developmental zero for eggs of *M. mexicanus* and *C. pellucida* is approximately 17° C.

General hatching of *M. mexicanus* and *C. pellucida* eggs under Montana conditions takes place during the first warm period in the spring when the maximum air temperatures are 24° C. (75.2° F.) or above for 3 to 5 successive days. Soil surface temperatures at time of hatching are generally 27° C. (80.6° F.) or above, and soil temperature at 2 inches, 23° C. (73.4° F.) or above.

The undercooling and freezing points of *M. mexicanus* eggs as determined by the thermo-couple method were respectively 21.3° and 19.5° C. Eggs of *C. pellucida* undercooled to –17° C. and froze at –15° C. When eggs were pierced by the thermo-couple point, the freezing point was raised 15.3° C. The formation of ice crystals in the eggs was not alone sufficient to kill them outright.

No eggs of either *M. mexicanus* or *C. pellucida* survived a 16-hour exposure to –30° C. (–22° F.) but at –25° C. (–13° F.)

35 to 50 per cent survived. Soil temperature records indicate that in nature such low temperatures rarely, if ever, occur at a depth of 2 inches.

The viability of eggs of both *M. mexicanus* and *C. pellucida* is lowered by an exposure of 3 or more hours at 45° C. (113° F.), and the eggs are killed by a 2-hour exposure at 50° C. (122° F.), or a 20-minute exposure at 60° C. (140° F.). Soil temperature records indicate that killing temperatures do not occur at the 2-inch level.

At constant temperatures the length of the nymphal stage and the percentage of total development per day of *M. mexicanus* were as follows: 22° C.—79 days, 1.26 per cent; 27° C.—42 days, 2.38 per cent; 32° C.—27 days, 3.66 per cent; 37° C.—23 days, 4.32 per cent. In *C. pellucida* they were as follows: 27° C.—43 days, 2.29 per cent; 32° C.—25 days, 4 per cent; 37° C.—21 days, 4.85 per cent.

Nymphs reared at alternating high and low temperatures developed faster at the high temperature than when held continuously at constant temperatures, the acceleration in rate of development being similar to that obtained in eggs held at alternating temperatures.

The daily activities of grasshoppers under natural conditions are to a large extent controlled by temperature. Detailed data are presented showing the air and soil surface temperatures at which the following activities take place: "beginning activity," "beginning normal activity," migration of nymphs, flight of adults, egg laying, feeding at poisoned bran mash, "climbing to escape heat," "beginning of clustering," "ending of activity." Data are also presented showing the temperature at which some of these activities take place in temperature cabinets.

Second and third instar nymphs of both *M. mexicanus* and *C. pellucida* survived a 24-hour exposure at –7° C. (19.4° F.), and about 50 per cent survived an exposure of the same length at –8° C. (17.6° F.), but all were killed by a 48-hour exposure. An exposure of 24 hours at –10° C. (14° F.) was necessary to kill adults of *M. mexicanus*, while adults of *C. pellucida* were killed by a 24-hour exposure at –9° C. (15.8° F.).

When the temperature is raised at the rate of approximately 1° C. in every five minutes, nymphs of *M. mexicanus* and *C. pellucida,* when confined in temperature cabinets, become greatly excited at 45° to 47° C. (113° to 116° F.), show first signs of heat rigor at 49° to 52° C. (120° to 125.6° F.), and at 53° to 54° C. (127.4° to 129.2° F.), are in complete heat rigor. Adults act the same except that complete heat rigor generally occurs at 56° to 58° C. (132.8° to 136.4° F.). Females are more heat resistant than males.

Temperature has a marked influence on the amount of food eaten per day, but although the nymphal period varied from 25 days at 37° C. to 94 days at 22° C. there was less than 5 per cent variation in the total amount of food consumed. At alternating temperatures *M. mexicanus* completed the nymphal stage in less time and on less food than at constant temperature.

During the first 20 days of adult life 10 specimens of *M. mexicanus,* held at 37° C., consumed 11,587 mgs. of dry matter, which was 2.5 times as much as the amount consumed by an equal number at 27° C. From this it is reasoned that grasshoppers will eat more food and therefore do more damage to crops during hot weather than during cool weather.

It was demonstrated that *M. mexicanus* females can far exceed the production of 2 egg pods, which was previously considered the usual number laid. One female caged in August laid 15 egg pods, and the average for 30 females was 8.8 egg masses. Temperatures ranging from 27° to 37° C. are favorable to maximum egg production in *M. mexicanus* and from 32° to 37° C. in the case of *C. pellucida.* It is suggested that years with high summer temperatures will provide many more hours for maximum egg laying than those with cool summers, and that temperature is therefore an important factor in relation to grasshopper abundance. Grasshoppers such as *M. mexicanus,* with high egg-laying capacities, can best take advantage of such favorable years.

In the case of *M. mexicanus* it was found that when reared at 22° and 27° C. there were always 6 nymphal instars, while at 32° and 37° C. there were only 5. *C. pellucida* passed through 5 instars at all temperatures at which it could be reared.

Temperature has a marked effect upon color, grasshoppers reared at high temperatures tending toward light ground colors with contrasting markings while low temperatures produce darker-colored individuals.

A higher percentage of *C. pellucida* eggs hatched in moderately damp soil than under very wet or very dry soil conditions. Submerging eggs of this species in water for a period of 110 days killed approximately 75 per cent.

When eggs of *M. mexicanus* were held at constant temperatures and constant relative humidities, a definite zone of optimum conditions was indicated. At 22° C. the highest percentage of eggs hatched at 80 per cent relative humidity, while at 27°, 32°, and 37° C. the optimum was 90 per cent. The higher the temperature the narrower was the range of relative humidity within which hatching took place.

Extremely low humidities retard the time of hatching. When exposed to low humidities, eggs of *C. pellucida* and *M. mexicanus* lose weight very rapidly. If the moisture content is lowered beyond 50 to 60 per cent the eggs are generally killed. Eggs dried out to a lesser extent regain their original weight when placed in damp sand, and at proper temperature conditions many of them will hatch. *M. mexicanus* eggs lose weight more rapidly at low humidities than eggs of *C. pellucida*.

Eggs from damp sand undercooled and froze at higher temperature than eggs from dry sand, and were also more susceptible to extremely high temperatures.

The time necessary to kill *C. pellucida* nymphs by submerging in water varied from 3 hours at 37° C. to 84 hours at 0° to 1° C.

Moisture indirectly affects grasshoppers by making conditions favorable for fungous and bacterial diseases. Data are given on moisture and temperature conditions during epidemics of disease known to have destroyed large numbers of grasshoppers.

Field observations and rearing experiments indicate that moisture may affect grasshoppers indirectly through their food supply, food of low moisture content having a tendency to produce larger and relatively longer-winged individuals than highly succulent food. The possibility that the Rocky Mountain locust *(M. spretus)* was merely a dry-weather, migratory phase of *M. mexicanus* is suggested.

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